BULLETIN OF MARINE SCIENCE, 43(1): 1–40, 1988

OSTEOLOGICAL DEVELOPMENT OF THE RED SNAPPER, *LUTJANUS CAMPECHANUS* (LUTJANIDAE)

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ABSTRACT

Osteological development of a series of 129 red snapper (Lutjanidae: *Lutjanus campechanus*) larvae, juveniles and adults (2.5 mm NL to 332 mm SL) is described from cleared and stained material. Emphasis is placed upon development of the vertebral column, ribs, fins and their supports, hyoid arch, branchial skeleton, mandibular arch, and opercular series. Cartilaginous neural arches and spines develop from anterior to posterior. Cartilaginous haemal arches and spines develop caudad at the time when neural arches develop dorsad, but haemal parapophyses develop rostrad. Ossification of neural and haemal arches and spines proceeds in the same direction as cartilaginous development. Ossification of centra is approximately in step with neural and haemal arch and spine ossification. Saddle-shaped ossifications on the notochord at the base of the neural and haemal arches are the first signs of centra ossification. Eight pairs of pleural ribs originate from cartilage and then ossify. Eight pairs of epipleural ribs ossify in the tissue of the myosepta. Notochord flexion starts in larvae between 3.9 and 4.8 mm NL. Four cartilaginous hypurals appear before flexion; hypural 5 develops after flexion. The sequence of spine and ray development for fins is as follows: spinous dorsal, pelvic, caudal, soft dorsal and anal, pectoral. Addition of spines and rays is caudad for the spinous, soft dorsal, and anal fins, from lateral to medial for the pelvic, from the midline outward for the caudal, and from dorsal to ventral for the pectoral. Dorsal fin spines are smooth during development, but pelvic spines have serration during parts of the larval and juvenile stages. All bones basic to the percoid caudal skeleton develop without fusion in adults, except the spinous dorsal fin distal radials are fused to the proximal radials. There was no fusion in the pectoral, pelvic, soft dorsal and anal fin support bones. The hyoid arches form initially in cartilage, but branchiostegal rays are of dermal origin. The branchial arches form in cartilage, gillrakers and toothpatches are of dermal origin, and the origin of toothplates is not clear. Bones of the upper jaw are dermal in origin, whereas the lower jaw originates from cartilage and has endochondral and epichondral ossifications. Meckel's cartilage is retained in the lower jaw in adults. In the opercular series only the preopercular develops spines in larvae. Preopercular spines are added to the interior shelf in juveniles and adults, so that it becomes serrated.

Red snapper (*Lutjanus campechanus*) are of importance to both commercial and recreational fisheries of the southeastern United States. During the last two decades recreational and commercial landings have steadily decreased (Bradley and Bryan, 1975; Arnold et al., 1978; Collins et al., 1980; Rabalais et al., 1980; Bohnsack and Harper, 1987). To better manage this fishery, more information on life history and development is needed (Arnold et al., 1978; Leis, 1987). The purpose of this paper is to add more information to the life history.

The genus *Lutjanus* occurs in all subtropical and tropical oceans and has 65 species (Allen, 1987). Rivas (1966) restricted *L. campechanus* as the Gulf red snapper occurring in the Gulf of Mexico and along the North American coast to Cape Hatteras. Rabalais et al. (1980) described laboratory-reared *L. campechanus* to 10 days and 2.8 mm NL, whereas Collins et al. (1980) described wild-caught larvae and juveniles from 4.0 mm NL to 22.4 mm SL. There are only a few descriptions of other *Lutjanus* larval species. Suzuki and Hioki (1979) characterized laboratory-reared *L. kasmira* to 3 days (3.2 mm TL). Richards and Saksena (1980) characterized laboratory-reared larvae and juveniles of the gray snapper *L. griseus*. Mori (1984) described wild-caught larvae and juveniles of *L. vitta* from the Sea of Japan. Fahay (1975) described two wild-caught postlarvae of *Lutjanus* sp. from the Atlantic coast of the U.S., and illustrated one, which we believe to be *L. campechanus* on the basis of the anal fin count. Leis and Rennis (1983) described a 7.7-mm postlarva of *Lutjanus*. *Rhomboplites aurorubens* is the only species of Lutjanidae other than *Lutjanus* for which larvae are described (Laroche, 1977). Leis (1987) lists described stages of lutjanid larvae in a table. According to this table, flexion to postflexion stages of *Caesio cuning* are described in Leis and Rennis (1983). We cannot find such a description unless their figure 27, p. 101, refers to *C. cuning*, but this is unclear.

Detailed adult osteology and developmental osteology have not been described for any species of Lutjanidae. Johnson (1981) discussed the relationships of lutjanids and associated families based on adult osteological and other characters. Mori (1984) discussed some osteological features in juvenile *L. vitta*, and Richards and Saksena (1980) described developmental osteology from four *L. griseus*.

Materials and Methods

A series of 129 *L. campechanus* larvae, juveniles and adults (2.5 mm NL to 332 mm SL) was measured for notochord length (NL) before and during flexion and for standard length (SL) after flexion following Potthoff et al. (1987). The whole series was then cleared and stained using the method of Potthoff (1984). The specimens were identified by the third author based on Collins et al. (1980). Larvae less than 4.0 mm NL are identified as *Lutjanus* sp. and only tentatively as *L. campechanus*. All specimens used in this study were captured in the northern or northwestern Gulf of Mexico. Capture localities and methods of capture for the larvae are given in Collins et al. (1980). Our larvae <4.0 mm NL came from the same localities, but were not included in the Collins et al. study. The juveniles came from trawling surveys and the two adults were bought in a fish house in Panama City, Florida.

For the caudal complex we use a composite terminology following Gosline (1961a, 1961b), Nybelin (1963) and Monod (1968). For the terminology of the branchial and hyoid arches, we follow McAllister (1968), Nelson (1969) and Rosen (1973). For the terminology of the mandibular arch, we follow Johnson (1981).

Osteological Development

Vertebral Column (Figs. 1–6, 11, Tables 1–3).—*Lutjanus campechanus* has 24 vertebrae (10 precaudal and 14 caudal). The large first anal pterygiophore immediately anterior to first haemal spine of anteriormost caudal centrum; only precaudal vertebrae support ribs; anteriormost neural arch and spine of first precaudal centrum and posteriormost two haemal arches and spines of 22nd and 23rd centra autogenous.

First (anteriormost) ventrally-directed parapophysis present on fifth or sixth precaudal centrum and first closed haemal arch on eighth centrum. Neural prezygapophyses found on all centra including urostyle, but neural postzygapophyses occur only on centra 2 to 22. Haemal prezygapophyses occur on caudal centra 14 or 15 to urostyle and haemal postzygapophyses on centra 10 or 11 to 21 or 22.

Smallest specimens, 2.5 and 2.8 mm NL, with no neural or haemal arches or spines along straight notochord. Development of cartilaginous neural arches and spines begins in some specimens at 2.9 mm NL, and all specimens 3.0 mm NL and larger, with neural arch and spine development. Addition of neural arches and spines from anterior to posterior. Cartilaginous haemal arch and spine development starts with anteriormost haemal arches and spines between 3.4 and 3.6 mm NL, when neural arch and spine development has reached area above developing haemal arches and spines. Addition of cartilaginous haemal arches and spines in posterior direction, but cartilaginous parapophyses added in anterior direction. Cartilaginous hypurals first appear in some specimens at 3.6 mm NL

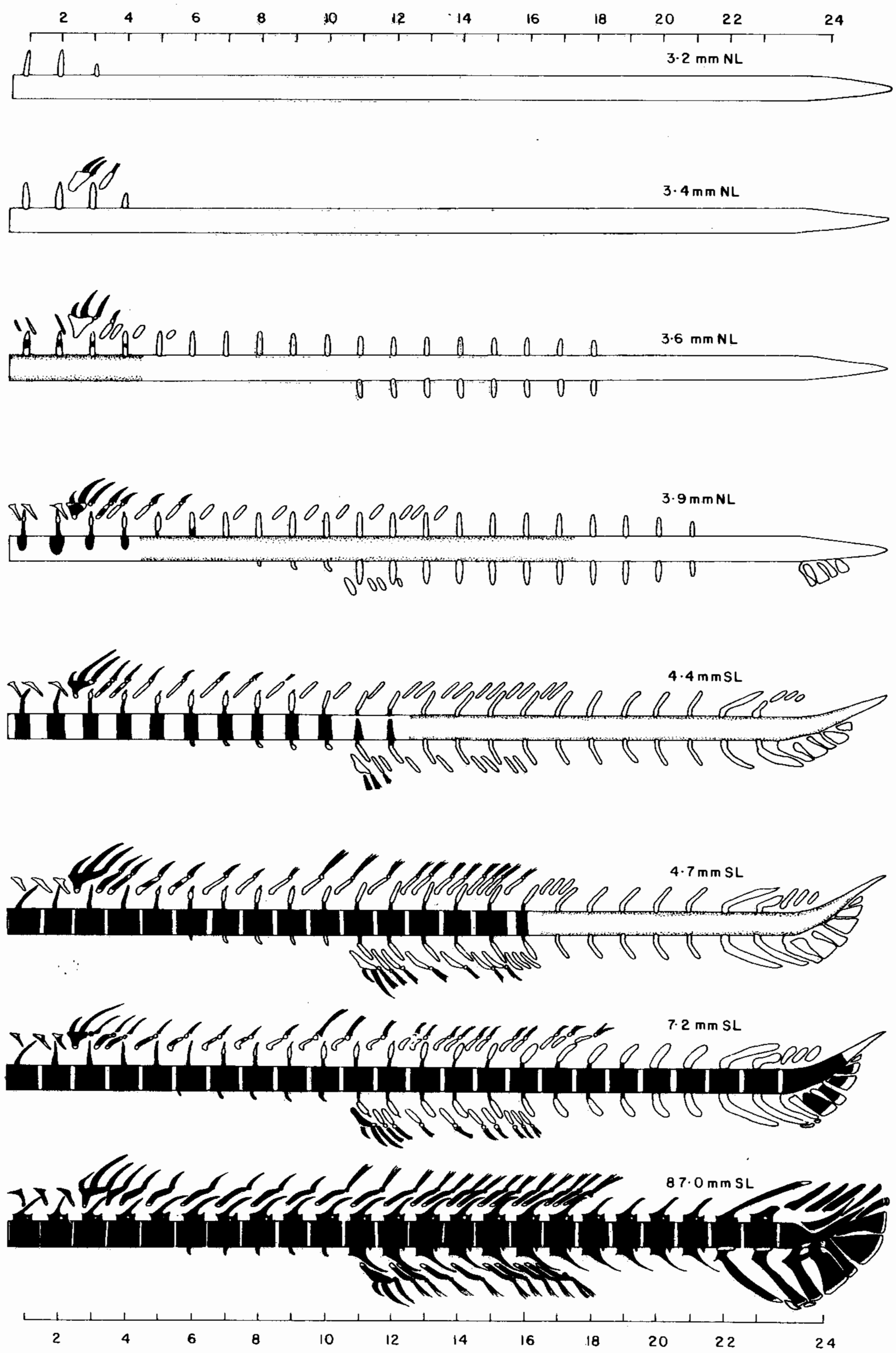

Figure 1. Semi-schematic representation of fin ray, fin support and vertebral column development in *Lutjanus campechanus*. Scales represent vertebral numbers. Cartilage, white; ossifying, stippled and blackened.

Table 1. Development of fin support and vertebral column counts from 115 cleared and stained *Lutjanus campechanus* larvae and juveniles (C = cartilage; O = ossifying)

NL or SL (mm)	Specimens (No.)	Neural arches and spines (No.) C	Neural arches and spines (No.) O	Haemal arches and spines (No.) C	Haemal arches and spines (No.) O	Predorsals (No.) C	Predorsals (No.) O
2.5	1	0	0	0	0	0	0
2.8	2	0	0	0	0	0	0
2.9	5	0–2	0	0	0	0	0
3.0	6	1–5	0	0	0	0	0
3.1	4	3, 5	0	0	0	0, 3	0
3.2	6	3–5	0	0	0	0	0
3.3	1	4	0	0	0	0	0
3.4	4	3, 4, 11	0, 1	0, 2	0	0, 3	0
3.5	3	3, 6, 12	0, 4	0, 6	0	0, 3	0
3.6	7	10, 14–16, 18, 19	1–5	7, 8, 10, 13	0	0, 3	0
3.7	2	17	6	13	0	3	0
3.8	4	14, 16, 18	1, 4, 6, 7	13	0	3	0
3.9	7	12, 15, 18, 19	4–6	9, 11, 13	0	3	0
4.0	2	14, 17	6, 9	13	0	3	0
4.1	3	14, 17	4, 6, 9	13	0	3	0
4.2	2	16, 17	6, 7	13	0	3	0
4.3	4	7, 14–16	7–9, 14	10, 13	0, 3	3	0
4.4	4	11, 13, 14, 16	7, 9, 10, 12	9, 11, 13	0, 2, 4	0, 3	0, 3
4.5	5	12–15	8–10, 13	10, 13	0, 3	0, 3	0, 3
4.6	4	7, 10, 13, 15	8, 10, 13, 16	9, 13	0, 4	3	0
4.7	4	7, 10, 15, 16	7, 8, 13, 16	8, 11, 13	0, 2, 5	3	0
4.8	3	5, 14, 15	8, 9, 18	6, 13	0, 7	2, 3	0, 1
4.9	2	7, 13	10, 16	7, 13	0, 6	3	0
5.0	4	6, 8, 12	11, 15, 17	5, 6, 8, 13	0, 5, 7, 8	3	0
5.1	2	6, 13	10, 17	6, 13	0, 7	3	0
5.2	1	5	18	5	8	3	0
5.3	2	5, 11	12, 18	5, 11	2, 8	3	0
5.4	1	14	9	13	0	3	0
5.6	1	3	20	3	10	0	3
5.7	2	6, 11	12, 17	6, 11	2, 7	3	0
5.8	1	7	16	6	7	0	3
5.9	1	8	15	8	5	3	0
6.0	1	3	20	3	10	3	0
6.3	1	3	20	3	10	3	0
6.4	1	2	21	1	12	0	3
6.5	1	1	22	1	12	3	0
6.6	1	1	22	0	13	0	3
6.9	1	5	18	6	7	3	0
7.1	1	0	23	0	13	0	3
7.2	1	4	19	4	9	0	3
7.9	1	0	23	0	13	0	3
8.3	1	1	22	0	13	0	3
9.1	1	1	22	0	13	0	3
9.5	1	0	23	0	13	0	3
13.0	1	0	23	0	13	0	3
21.0	1	0	23	0	13	0	3
22.4	1	0	23	0	13	0	3

when about 19 neural and 9 haemal spines present. Addition of neural and haemal spines belonging to caudal complex (PU_2 and PU_3) in anterior direction. All neural and haemal arches and spines present in some specimens at 3.6 mm NL and in all by 4.2 mm NL or SL. Notochord flexion occurs over size range from 3.9 to

Table 1. Continued

Spinous dorsal		Soft dorsal fin		Anal fin		Ossifying central	
No. proximal C	No. radials O	No. proximal C	No. radials O	No. proximal C	No. radials O	No. precaudal	No. caudal
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0–2	0	0	0	0	0	0	0
0, 4	0	0	0	0	0	0	0
0, 2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0
0, 4	0	0	0	0	0	0	0
0, 5, 6	0	0	0	0	0	0	0
5–8	0–2	0	0	0, 6, 8	0	0, 3, 4	0
6, 7	1, 2	9, 10	0	5, 9	0	0, 5	0
5, 6	1, 2	0, 5, 10	0	0, 4, 6	0	0, 6	0
5, 6, 8	0, 2, 3	2, 4, 6, 11	0	0, 3, 4, 7	0	0, 4	0
5	3	10, 13	0	7, 10	0	5, 10	0
5, 7	1, 3	1, 11, 14	0	0, 8, 10	0	0, 5, 10	0, 2
4, 6	2, 4	11, 12	0	0, 7	0	3, 6	0
4, 5	3, 4	12–14	0	9, 10	0	6, 10	3, 7
2, 4, 5	3, 4, 6	10–12, 14	0	8–10	0	6, 10	0, 1, 4
2–5, 7	1, 3–6	11, 13, 14	0	9, 10	0	6, 7, 10	0, 3, 4, 6
2, 4	4, 6	12–14	0	9, 10	0, 1	8, 10	0, 3, 5, 6
3–5	3–5	14	0	9, 10	0, 1	8, 10	0, 5
3, 5	3, 5	13, 14	0	9	0, 1	9, 10	0, 2, 10
3, 4	4, 5	13, 14	0	9	0, 1	10	4, 6
1–4	4–7	13, 14	0	7–9	1, 3	10	5, 7, 10
3, 5	3, 5	14	0	9, 10	0, 1	10	7, 8
4	4	14	0	9	1	10	8
2, 3	5, 6	14	0	8, 9	1, 2	10	8, 9
4	4	13	0	10	0	10	4
1	7	14	0	9	1	10	13
1, 3	5, 7	14	0	9, 10	0, 1	10	7, 11
2	6	14	0	9	1	10	13
1	7	14	0	9	1	10	10
1	7	14	0	9	1	10	10
1	7	14	0	9	1	10	12
3	5	14	0	9	1	10	13
1	7	14	0	9	1	10	13
0	8	14	0	9	1	10	13
2	6	14	0	9	1	10	13
0	8	13	1	8	2	10	13
0	8	13	1	9	1	10	13
0	8	11	2	7	2	10	13
0	8	12	2	7	3	10	13
0	8	12	2	8	2	10	13
0	8	12	2	6	4	10	13
0	8	9	5	5	5	10	13
0	8	0	14	0	10	10	13
0	8	0	14	0	10	10	13

4.8 mm. Larvae in this range have unflexed, partially flexed or fully flexed notochord.

Ossification of vertebral column starts anteriorly with neural arches and spines and notochord at 3.4 to 3.6 mm NL and proceeds in posterior direction. Vertebral column ossification complete between 7.1 and 7.9 mm SL. Notochord ossification

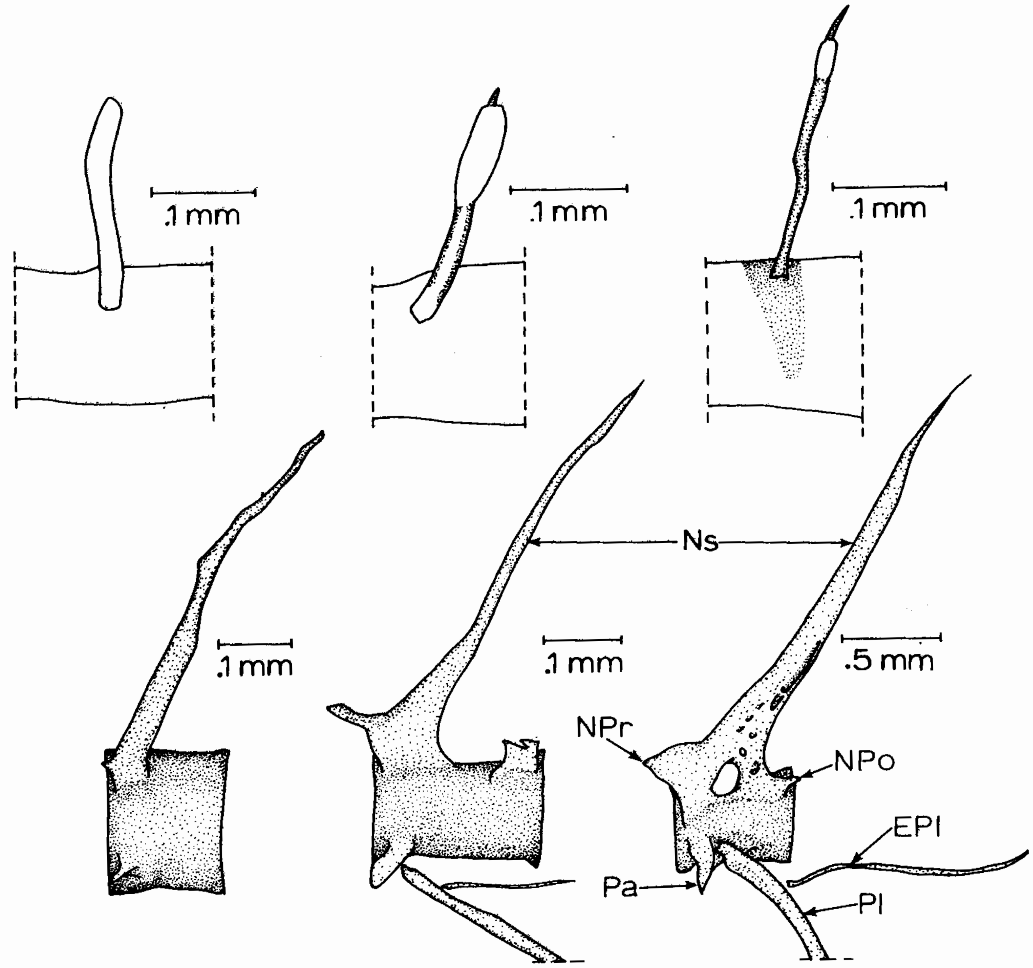

Figure 2. Development of 5th precaudal vertebra in *Lutjanus campechanus,* left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.5, 3.9, 4.1, 6.6, 13.0, 28.3. EPl, epipleural rib; NPo, neural postzygapophysis; NPr, neural prezygapophysis; Ns, neural spine; Pa, parapophysis; Pl, pleural rib. Cartilage, white; ossifying, stippled.

starts with formation of thin hyaline layer of bone around notochord followed by saddle-shaped ossifications beneath neural or above haemal arches. Finally, saddles of bone extend and coalesce to form individual centra. Hypural cartilages start to ossify before ossification of neural and haemal arches and spines reaches hypural complex, although notochord surrounded by thin layer of bone to urostyle. Ossification of individual neural and haemal arches and spines starts at bases of arches and proceeds distally. Bone also forms at tips of cartilaginous neural and haemal spines, at first resembling bony flagella. Flagella expand distally and grow into neural spines. Neural and haemal arch ossifications also grow distally, joining with flagellum-like ossifications, and forming completely ossified neural and haemal arches and spines.

Epipleural and Pleural Ribs (Figs. 2, 3, Table 3).—*Lutjanus campechanus* has eight pairs of epipleural and eight pairs of pleural ribs. Anteriormost epipleural rib articulates with neural prezygapophysis of first neural spine. Second epipleural rib articulates at base of second neural spine and third to eight epipleural ribs

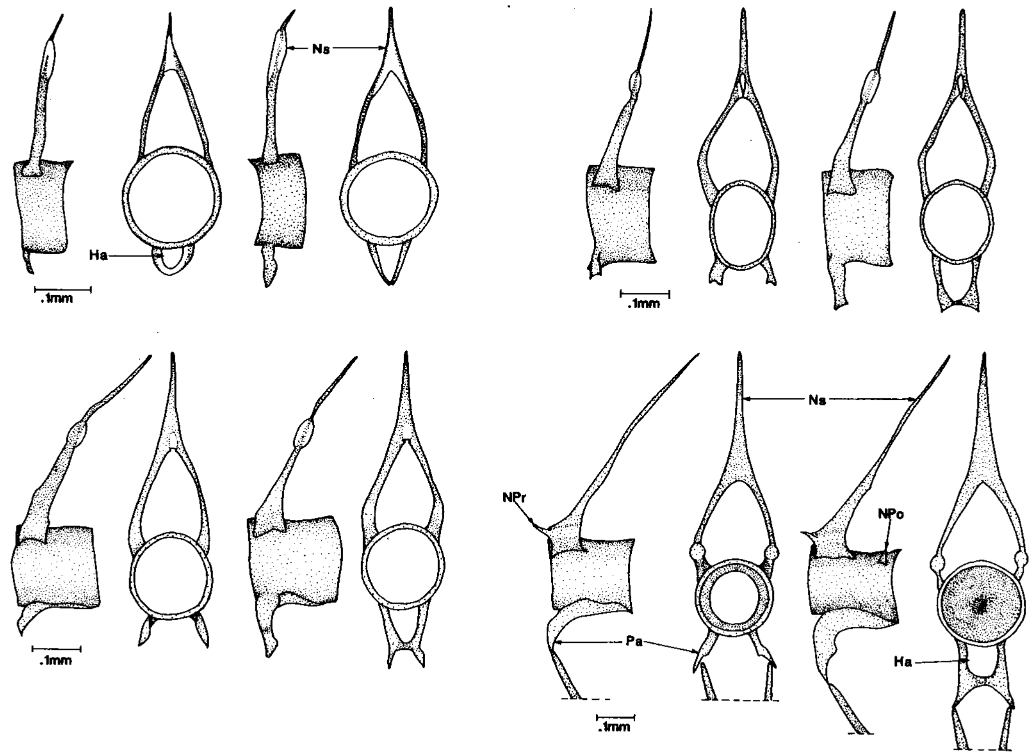

Figure 3. Development of 7th and 8th precaudal vertebrae in *Lutjanus campechanus*. The 7th vertebra is on the left, the 8th vertebra on the right. For each vertebra, the left lateral view is to the left and the anterior view to the right. Top left to bottom right specimens' lengths in mm NL or SL are: 4.6, 4.8, 7.1, 9.5. Ha, first haemal arch. For other abbreviations, see Figure 2.

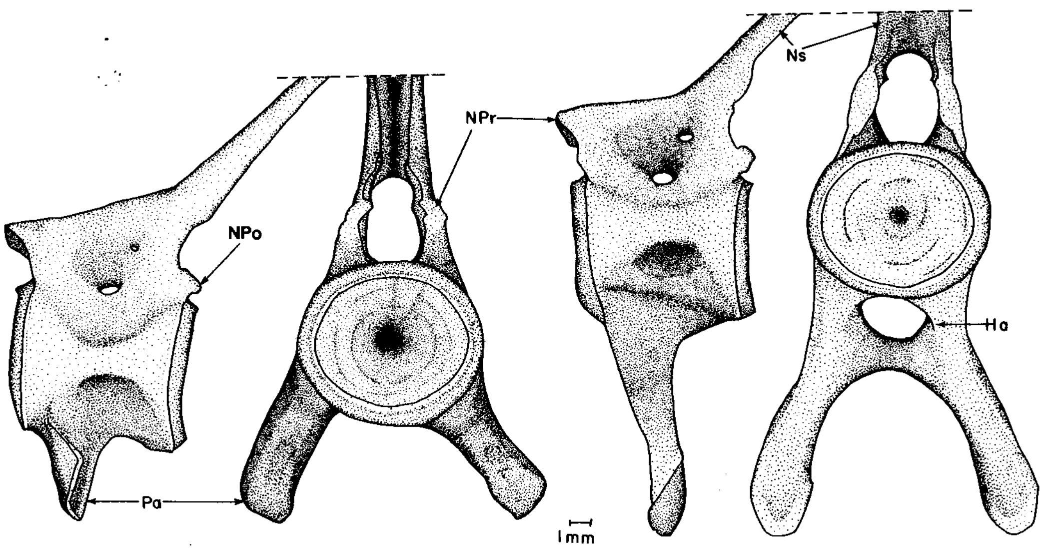

Figure 4. Views of two vertebrae from an adult 332-mm SL *Lutjanus campechanus*. From left to right: left lateral view and anterior view of 7th precaudal vertebra, left lateral view and anterior view of 8th precaudal vertebra. For abbreviations, see Figures 2 and 3.

Table 2. Fin, spine and ray counts of 117 *Lutjanus campechanus* larvae, juveniles and adults cleared and stained before counting. (The sum of unflexed and flexed specimens does not always correspond to number of specimens because of some damaged samples)

NL or SL (mm)	Specimens (No.)	Caudal fin rays Secondary upper	Principal upper/lower	Secondary lower	Spinous dorsal-fin spines–rays
3.0	5	0	0	0	0
3.1	3	0	0	0	0; II
3.2	6	0	0	0	0; II
3.3	1	0	0	0	0
3.4	4	0	0	0	0; III
3.5	3	0	0	0	0; III; IV
3.6	7	0	1/1	0	III–VI
3.7	2	0	1/1, 4/4	0	VI; VIII
3.8	4	0	0, 3/3	0	V–VIII
3.9	6	0	0, 1/1, 3/3	0	II; V–VII
4.0	2	0	4/4, 5/5	0	VII,2; X
4.1	3	0	0, 4/4, 6/6	0	VI; VIII; X
4.2	2	0	4/4, 4/5	0	VIII
4.3	4	0	5/5, 5/6, 6/6, 9/8	0, 1	VIII,2; X
4.4	4	0	4/3, 5/5, 6/6, 6/7	0	VIII; VIII,2; IX,1
4.5	5	0	3/3, 4/4, 7/8, 8/8, 9/8	0	VIII; VIII,2; IX,1
4.6	4	0	5/4, 9/8	0, 1	VIII,2; IX; IX,1
4.7	4	0	5/4, 9/8	0	VIII,2; IX,1
4.8	3	0, 1	4/4, 9/8	0, 2	IX; X
4.9	2	0	8/8, 9/8	0, 1	IX,1
5.0	3	0	9/8	0, 1	IX,1; X
5.1	2	0	9/8	1	IX,1
5.2	1	0	9/8	1	IX,1
5.3	2	0	9/8	1	IX,1
5.4	1	0	8/8	0	IX,1
5.6	1	1	9/8	2	IX,1
5.7	2	0	9/8	1	IX,1; X
5.8	1	2	9/8	2	IX,1
5.9	1	1	9/8	2	IX,1
6.0	1	0	9/8	1	IX,1
6.3	1	1	9/8	2	IX,1
6.4	1	2	9/8	2	IX,1
6.5	1	2	9/8	2	IX,1
6.6	1	1	9/8	3	IX,1
6.9	1	2	9/8	3	IX,1
7.1	1	2	9/8	2	IX,1
7.2	1	0	9/8	0	X
7.9	1	4	9/8	4	X
8.3	1	4	9/8	4	X
9.1	1	6	9/8	6	X
9.5	1	—	—	—	X
13.0	1	9	9/8	9	X
21.0	1	10	9/8	11	X
22.4	1	10	9/8	10	X
28.3	1	11	9/8	11	X
37.4	1	10	9/8	10	X
56	1	9	9/8	10	X
70, 72, 78	4	10, 11	9/8	10	X
87, 96, 98	3	9, 10	9/8	10	X
105, 120	2	9, 10	9/8	10	X
300, 332	2	10	9/8	10	X

Table 2. Continued

Soft dorsal-fin rays	Anal fin, spines–rays	Pectoral fin rays Left/right	Pelvic fin rays Left	Pelvic fin rays Right	Number of specimens Unflexed/flexed /flexing,
0	0	0/0	0	0	5/0
0	0	0/0	0	0	3/0
0	0	0/0	0	0	6/0
0	0	0/0	0	0	1/0
0	0	0/0	0; I,0	0; I,0	4/0
0	0	0/0	0; I,1; I,2	0; I,1; I,2	3/0
0	0	0/0	I,0–I,3	I,0–I,3	7/0
0	0	0/0	I,2; I,3	I,2; I,3	2/0
0	0	0/0	I,2; I,3	I,2; I,3	4/0
0	0	0/0	0; I,2; I,3	0; I,2; I,3	5/1
0, 2	0; II,3	0/0	I,3; I,4	I,3; I,4	1/1
0, 3	0; II,4	0/0	I,2–I,4	I,2–I,4	2/1
0	0	0/0	I,3; I,4	I,3; I,4	2/0
0, 8, 13	3; II,5–II,8	0/0	I,3–I,5	I,3–I,5	1/3
0, 7, 9	0; 3; II,6	0/0	I,3	I,3	2/2
0, 10, 11	0; II,6–II,8	0/0	I,3; I,4	I,3; I,4	2/3
0, 7, 10, 12	II; II,6; II,8	0, 2/0, 3	I,3–I,5	I,3–I,5	1/2
0, 11–13	4; II,7–II,9	0, 2, 4/0, 4	I,3–I,5	I,3–I,5	1/3
0, 2, 14	3; I,2; II,10	0, –/0, 8	I,3–I,5	I,3–I,5	2/1
10, 13	II,6; II,9	0, 4/0, –	I,4; I,5	I,4; I,5	0/2
11, 12, 14	II,8; II,9	6, 3/7, 1	I,5	I,5	0/3
13	II,8; II,10	0, 3/0, 3	I,5	I,5	0/2
13	II,10	5/4	I,5	I,5	0/1
14	II,10	6, –/5, 3	I,5	I,5	0/2
10	II,7	2/2	I,4	I,4	0/1
14	II,10	11/10	I,5	I,5	0/1
13, 14	II,9; II,10	4, 9/5, 8	I,5	I,5	0/2
14	III,9	12/–	I,5	I,5	0/1
14	II,10	–/9	I,5	I,5	0/1
14	II,10	–/–	I,5	I,5	0/1
14	II,10	9/8	I,5	I,5	0/1
14	II,10	11/12	I,5	I,5	0/1
14	III,9	–/–	I,5	I,5	0/1
14	II,10	9/10	I,5	I,5	0/1
14	III,9	–/12	I,5	I,5	0/1
14	III,9	12/11	I,5	I,5	0/1
14	III,9	13/13	I,5	I,5	0/1
13	III,8	14/–	I,5	I,5	0/1
14	III,9	16/–	I,5	I,5	0/1
14	III,9	16/15	I,5	I,5	0/1
14	III,9	–/–	I,5	I,5	0/1
14	III,9	18/18	I,5	I,5	0/1
14	III,9	17/17	I,5	I,5	0/1
14	III,9	17/17	I,5	I,5	0/1
14	III,9	16/16	I,5	I,5	0/1
14	III,9	17/17	I,5	I,5	0/1
14	III,9	17/17	I,5	I,5	0/1
14	III,9	17/17	I,5	I,5	0/3
14	III,9	17/17	I,5	I,5	0/3
14, 15	III,9	17, 18/17	I,5	I,5	0/2
13, 14	III,8; III,9	17/17	I,5	I,5	0/2

Table 3. Development of gillrakers, branchiostegal rays, ribs, first haemal arch and preopercular spines in 129 cleared and stained larvae, juveniles and adults of *Lutjanus campechanus*

NL or SL (mm)	Speci-mens (No.)	Number left side first arch gillrakers*					Branchiostegal rays		Pairs of ribs found on vertebra number (number of rib pairs)			First closed haemal arch on vertebra number	Preopercular spines	
		Epi-bran-chial	Angle	Cerato-branchial	Hypo-branchial	Total	Left side (No.)	Right side (No.)	Epipleural	Pleural: Cartilage	Pleural: Ossified		Outer shelf (No.)	Inner shelf (No.)
2.5	1	0	0	0	0	0	0	0	0	0	0	Not developed	2	3
2.8	2	0	0	0	0	0	1	1	0	0	0	Not developed	2, 3	3
2.9	5	0	0	0	0	0	1–3	1–3	0	0	0	Not developed	2, 3	3, 4, 5
3.0	6	0	0	0, 2	0	0, 2	3, 4	3, 4	0	0	0	Not developed	2, 3	3, 4
3.1	4	0	0	0, 2, 3	0	0, 2, 3	3–5	3–5	0	0	0	Not developed	2–4	3–5
3.2	6	0	0	0	0	0	4, 5	4, 5	0	0	0	Not developed	2, 3	4, 5
3.3	1	0	0	0	0	0	2	2	0	0	0	Not developed	3	4
3.4	4	0	0	0, 3, 4	0	0, 3, 4	4, 5	4, 5	0	0	0	Not developed	2, 3	4, 5
3.5	3	0	0, 1	0, 5	0	0, 6	2, 6	2, 6	0	0	0	Not developed	2, 3	3, 5
3.6	7	0	0, 1	3–6	0	3–7	4–6	4–6	0	0	0	7, 9	2, 3, 4	4, 5
3.7	2	0	1	6	0	7	6, 7	6, 7	0	0	0	8	3	5
3.8	4	0	0, 1	4, 6, 7	0	5, 7, 9	6, 7	6, 7	0	0	0	7, 10, 11	3	5
3.9	7	0	0, 1	3, 5, 6, 7	0	3, 6, 7, 8	5, 6, 7	5, 6, 7	0	0	0	7, 11	2, 3	4, 5
4.0	2	1	1	7, 8	0	9, 10	7	7	0	0	0	7	1, 3	5
4.1	3	0, 2	1	6, 7	0	7, 8, 10	6, 7	6, 7	0	0	0	7, 9	3	5
4.2	2	0, 1	1	6, 8	0	7, 10	6, 7	7	0	0	0	7	1, 3	5
4.3	4	1, 2	1	7, 8	0	9, 10, 11	7	7	0	0	0	7, 8	3	5
4.4	4	1, 2	1	7, 8	0	9, 10, 11	6, 7	7	0	0	0	7, 8	3, 4	5
4.5	5	1	1	7, 8	0	9, 10	7	7	0	0	0	7, 8	3	5
4.6	4	1	1	7, 8	0	9, 10	7	7	0	0	0	7, 8	2, 3	5
4.7	4	1, 2	1	8	0	10, 11	7	7	0	0	0	7, 8	3	6
4.8	3	1, 2	1	7, 8	0, 1	9, 12	7	7	0	0	0	8	3	5, 6
4.9	2	1, 2	1	8	0, 1	10, 12	7	7	0	0	0	7, 8	3	5, 6
5.0	4	2, 3	1	8	0	11, 12	7	7	0	0	0	8	3, 4, 5	5, 6
5.1	2	2	1	8	0	11	7	7	0	0	0	8	3, 4	5, 7
5.2	1	2	1	8	0	11	7	7	0	0	0	8	3	6
5.3	2	2	1	8	1	12	7	7	0	0	0	8	2	6
5.4	1	2	1	8	0	11	7	7	0	0	0	7	3	5
5.6	1	3	1	8	1	13	7	7	0	0	0	8	4	6

Table 3. Continued

NL or SL (mm)	Specimens (No.)	Number left side first arch gillrakers*					Branchiostegal rays		Pairs of ribs found on vertebra number (number of rib pairs)			First closed haemal arch on vertebra number	Preopercular spines	
		Epibranchial	Angle	Ceratobranchial	Hypobranchial	Total	Left side (No.)	Right side (No.)	Epipleural	Pleural			Outer shelf (No.)	Inner shelf (No.)
										Cartilage	Ossified			
5.7	2	2, 3	1	8	0, 1	11, 13	7	7	0	0	0	8	3	6
5.8	1	3	1	8	1	13	7	7	0	0	0	8	4	6
5.9	1	3	1	8	1	13	7	7	0	0	0	8	4	6
6.0	1	2	1	8	1	12	7	—	0	0	0	8	4	6
6.3	1	3	1	8	1	13	7	7	0	0	0	8	4	6
6.4	1	3	1	8	2	14	7	—	0	0	0	9	4	7
6.5	1	3	1	8	2	14	7	—	0	0	0	8	4	7
6.6	1	3	1	8	2	14	7	7	0	0	0	8	4	6
6.9	1	3	1	7	2	13	7	7	0	0	0	8	4	6
7.1	1	4	1	8	2	15	7	7	Some pleurals present, damage			8	4	6
7.2	1	3	1	8	3	15	7	7	0	3–6 (4)	0	8	4	7
7.9	1	4	1	8	2	15	7	7	0	4–8 (5)	3 (1)	8	4	6
8.3	1	4	1	8	2	15	7	—	1,2 (2)	7, 8 (2)	3–6 (4)	8	Damage	6
9.1	1	3	1	8	2	14	7	7	1,2 (2)	8, 9 (2)	3–7 (5)	8	Damage	6
9.5	1	3	1	8	2	14	—	7	1,2 (2)	9 (1)	3–8 (6)	8	4	7
13.0	1	5	1	8	3	17	7	7	1–7 (7)	10 (1)	3–9 (7)	8	3	7
21.0	1	5	1	8	3	17	7	7	1–8 (8)	0	3–10 (8)	8	0	20
22.4	1	7	1	8	3	19	7	7	1–8 (8)	0	3–10 (8)	8	0	31
28.3	1	7	1	8	4	20	7	7	1–8 (8)	0	3–10 (8)	8	0	32
37.4	1	7	1	8	4+2†	22	7	7	1–8 (8)	0	3–10 (8)	8	0	48
56	1	7	1	8	4+2†	22	7	7	1–8 (8)	0	3–10 (8)	8	0	51
70, 72, 78	4	7	1	8	4+1, 4+2†	21, 22	7	7	1–8 (8)	0	3–10 (8)	8	0	59–72
87, 96, 98	3	6, 7	1	8	4+1, 4+2†	20, 21, 22	7	7	1–8 (8)	0	3–10 (8)	8	0	64–80
105, 120	2	7	1	8	4+2†	22	7	7	1–8 (8)	0	3–10 (8)	8	0	84–96
300, 332	2	7, 8	1	8	4+1, 4+2†	22	7	7	1–8 (8)	0	3–10 (8)	8	0	96–128

* Includes toothpatches.
† Numbers after the plus refer to rakers found on tissue anterior to hypobranchials.

articulate with their respective pleural ribs, short distance proximal to pleural rib's distal ends. Pleural ribs articulate with parapophyses of third to tenth centra. Pleural ribs of ninth and tenth centra with no epipleural ribs. Cartilaginous pleural ribs first develop at 7.1 mm SL anteriorly and are added posteriorly. Ossification of pleural ribs starts at 7.9 mm SL anteriorly and proceeds in posterior direction. All eight pairs of pleural ribs develop by 13.0 mm SL and ossified between 13.0 and 21.0 mm SL. Epipleural ribs develop first at 8.3 mm SL anteriorly in connective tissue of myosepta directly as bone. Full complement of eight pairs of epipleural ribs attained between 13.0 and 21.0 mm SL.

Caudal Fin (Fig. 6, Tables 2, 4).—Adult *L. campechanus* with (9–11) + 9/8 + (10 or 11) caudal fin rays. Principal caudal rays with count of 1/1 first appear ventral to unflexed notochord on hypurals 2 and 3 in some 3.6 mm NL larvae. Rays added rostrad and caudad before flexion, but ventrad and dorsad just after flexion when full count of 9/8 principal rays attained in specimens ranging from 4.3 to 4.9 mm SL. Ventral secondary caudal ray first develops after full flexion and first dorsal secondary ray develops concurrently with the second ventral secondary ray. Secondary caudal rays first appear at 4.3 mm SL, and all specimens 5.6 mm SL and larger with at least one ventral secondary ray developed. Maximum caudal fin ray counts attained between 13.0 and 21.0 mm SL. Rays supported by bones articulating with 3 centra, PU_3, PU_2, and urostyle, and by radial cartilage. Principal caudal rays supported by hypurals 1 to 5, by parhypural and by haemal spine of preural centrum 2. Distribution of principal rays on caudal complex bones shown in Table 4. Procurrent spur (Johnson, 1975) not present.

Caudal Fin Supports (Figs. 1, 6, 7, Table 5).—Caudal complex of adults exhibits no fusion during ontogeny and has following bones: preural centrum 3 with ankylosed neural arch and spine and autogenous haemal arch and spine; preural centrum 2 with specialized neural arch and autogenous haemal arch and spine; urostyle with 3 epurals and 2 uroneurals dorsad, 5 hypurals posteriad and 1 parhypural postero-ventrad. Two radial cartilages present, anterior one ventrad between haemal spines of preural centra 2 and 3, and posterior one between haemal spine of preural centrum 2 and parhypural. Another radial cartilage present postero-dorsally to hypural 5. All hypurals, parhypural, haemal spines of preural centra 2 and 3, neural spine of preural centrum 3, and epurals with cartilaginous distal margins.

Specimens between 2.5 and 3.8 mm NL with straight notochords. Flexion occurs in some larvae 3.9 to 4.8 mm SL. All larvae 4.9 mm SL and larger with a flexing or flexed notochord. Separate cartilaginous hypurals 1–3 and parhypural first develop at 3.6 mm NL ventral to straight notochord. In some specimens specialized neural arch and haemal spine of preural centrum 2 and neural and haemal spines of preural centrum 3 also present. Hypural 4 develops posterior to and after hypural 3 before notochord flexion. During and after notochord flexion, small cartilaginous hypurals and three epurals develop. Anterior and middle epurals develop first, then posterior epural added. Parhypural and hypurals 1 and 2 develop as separate pieces of cartilage, but fuse proximad during notochord flexion. Parhypural and hypural 1 cartilages fuse first, followed by fusion of hypural 1 with hypural 2 cartilage. Hypurals 3–5 separate in cartilaginous state.

Ossification of caudal complex first starts with urostyle and hypurals 1–4 between 4.8 and 6.5 mm SL, followed by ossification of parhypural, which starts with parhypurapophysis between 5.1 and 7.9 mm SL. Next, anterior uroneural develops by ossification from connective tissue (dermal origin) between 5.3 and 8.3 mm SL; followed by ossification of preural centra 2, 3 between 5.6 and 6.4

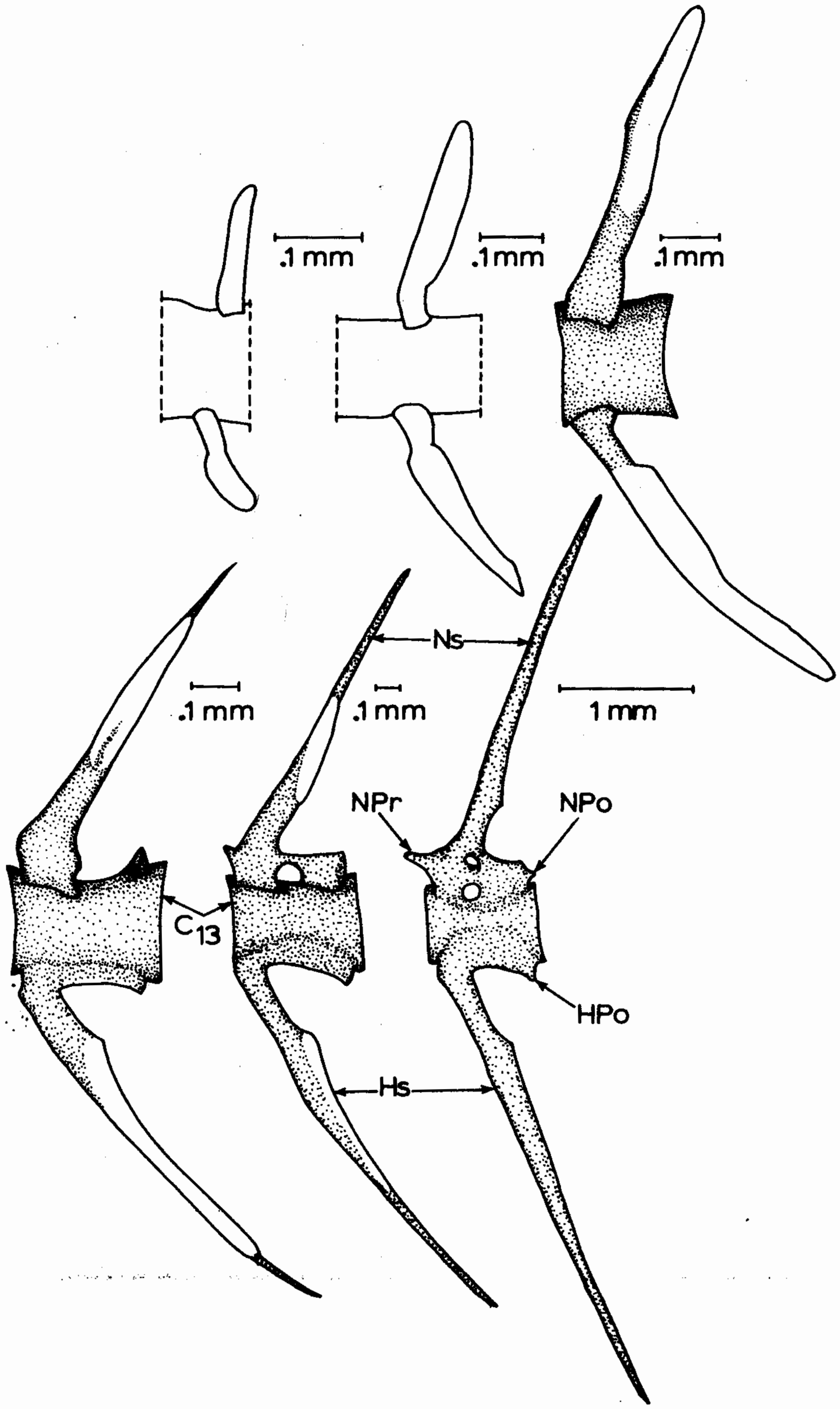

Figure 5. Development of 13th vertebra (3rd caudal) in *Lutjanus campechanus*, left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.5, 4.1, 6.6, 9.5, 13.0, 28.3. C, centrum; HPo, haemal postzygapophysis; Hs, haemal spine. For other abbreviations, see Figure 2.

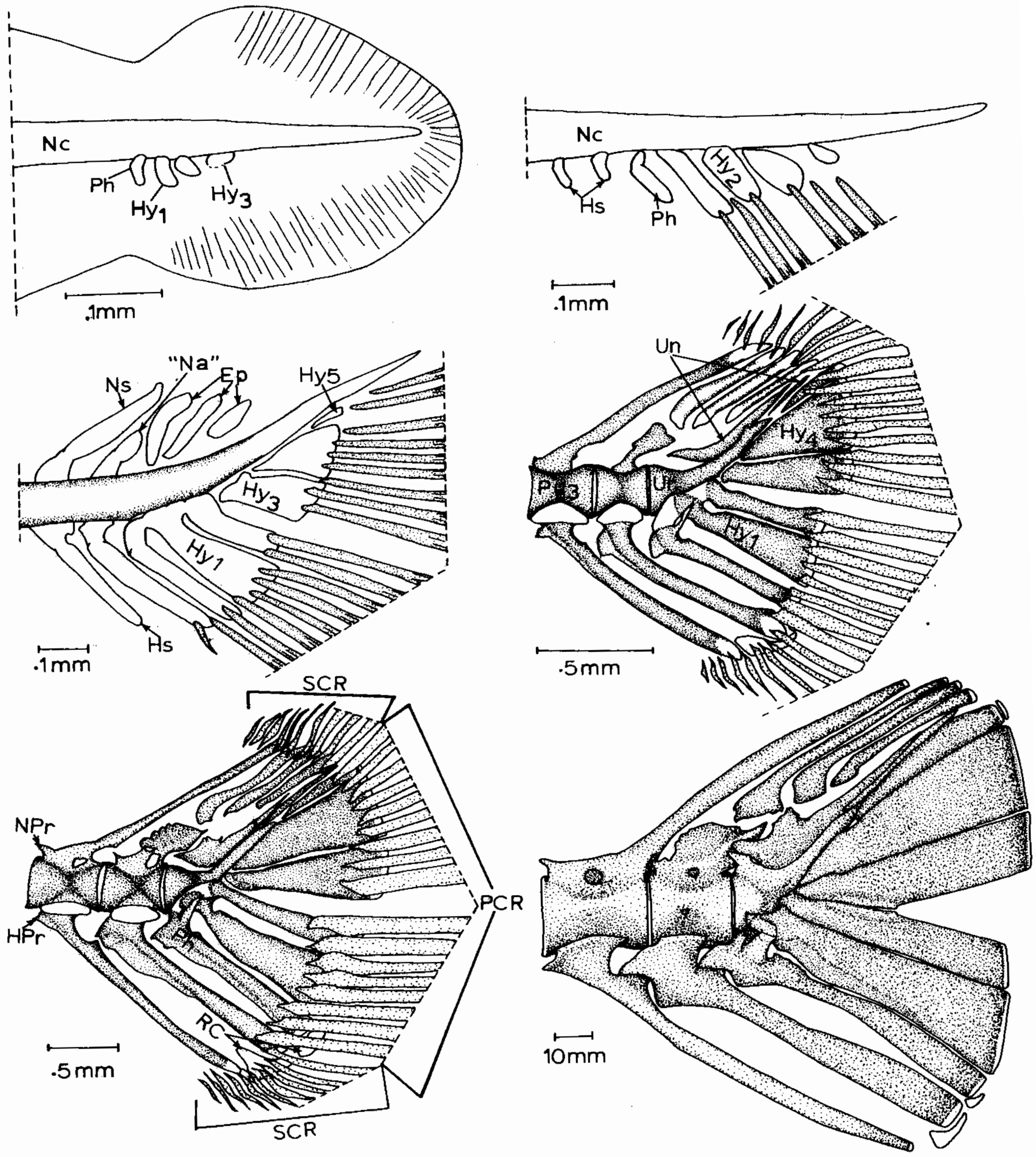

Figure 6. Development of the hypural complex in *Lutjanus campechanus,* left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.9, 3.7, 5.2, 13.0, 22.4, 332. Ep, epural; HPr, haemal prezygapophysis; Hs, haemal spine; Hy, hypural; "Na," specialized neural arch; Nc, notochord; NPr, neural prezygapophysis; Ns, neural spine; PCR, principal caudal rays; Ph, parhypural; Pu, preural centrum; RC, radial cartilage; SCR, secondary caudal rays; Un, uroneural; Ur, urostyle. Cartilage, white; ossifying, stippled.

mm SL, hypural 5 between 5.9 and 9.5 mm SL, neural and haemal spines of preural centrum 3 between 6.4 and 7.9 mm SL, and haemal spine of preural centrum 2 between 6.6 and 7.9 mm SL. Specialized neural arch of preural centrum 2 ossifies between 7.1 and 9.5 mm SL. Three epurals and small posterior uroneural last to ossify between 9.5 and 13.0 mm SL, size range for which specimens not available.

Anterior ventral radial cartilage between haemal spines of preural centra 3 and

Table 4. Distribution of principal caudal rays on the hypural bones in 52 *Lutjanus campechanus* larvae and juveniles (4.3–120 mm SL) (PU = preural centrum)

	Number principal caudal rays						
	0	1	2	3	4	5	6
Hypural 5		27	23	2			
Hypural 4					13	35	4
Hypural 3			20	31	1		
Hypural 2	1	25	26				
Hypural 1				10	40	2	
Parhypural		19	33				
Space between parhypural and haemal spine of PU_2	27	25					
Haemal spine–PU_2	24*	26*					

* A secondary caudal ray also articulated with the haemal spine of PU_2.

2 develops first in specimens between 5.9 and 6.5 mm SL, followed by posterior ventral radial cartilage between haemal spine of preural centrum 2 and parhypural in specimens between 7.2 and 9.1 mm SL. Dorsal radial cartilage above hypural 5 last to develop in size range (9.5–13.0 mm SL) for which no specimens available.

Pectoral Fin and Supports (Fig. 8, Tables 2, 6).—Adult pectoral-fin ray count 16 to 18 rays, but usually 17. Only in 1 of 17 juveniles and adults with full count did left side fin-ray count differ from right side by one ray. In larvae with incomplete pectoral fin-ray counts, left side often differs from right side count; usually by one ray. Difference of two or three rays rarely present. Pectoral fin rays start to develop during notochord flexion in some 4.6-mm SL specimens in pectoral finfold above cartilaginous blade. Rays first appear at dorsal-most edge of blade and added around edge in ventral direction. Adult counts attained between 9.5 to 13.0 mm SL, size range for which no specimens available.

Adult pectoral girdle including suspensorium with following bones on each side: two supratemporal-intertemporals, one posttemporal, one supracleithrum, one cleithrum, two postcleithra, one scapula and coracoid connected by cartilage, and four proximal radials. In addition, single distal radial cartilage present within open base of each fin ray. Two supratemporal-intertemporal bones and posttemporal bone accommodate part of laterosensory canal.

Our smallest 2.5-mm NL specimen already with bony cleithrum, coraco-scapular cartilage and cartilaginous blade. Cleithrum at first long and rod-shaped but develops broad triangular-shaped shelf (posterior process) dorsad and broad shelf area ventrad. Coraco-scapular cartilage first with long dorsal and posterior process and short anterior process. During ontogeny dorsal process remains at same relative length, posterior process shortens relatively and anterior process lengthens relatively. Foramen forms in dorsal process before notochord flexure, which becomes scapular foramen upon ossification, starting between 5.0 and 6.2 mm SL. Ventral half of dorsal process and anterior process ossify to coracoid, beginning between 4.8 and 6.2 mm SL. In adults scapula and coracoid joined by thin strips of cartilage. Cartilaginous pectoral fin blade first cleaves at center between 3.8 and 4.2 mm NL or SL, then dorsad between 4.0 and 4.5 mm NL or SL and last ventrad between 5.0 and 7.1 mm SL. During ontogeny cleavages extend dorsad and ventrad to margins of blade forming cartilaginous proximal radials. Proximal radials last pectoral fin supports to ossify between 9.1 and 13.0 mm SL; distal radials, which remain cartilaginous, originate from blade margin.

Supracleithrum and posttemporal bones of dermal origin. Supracleithrum de-

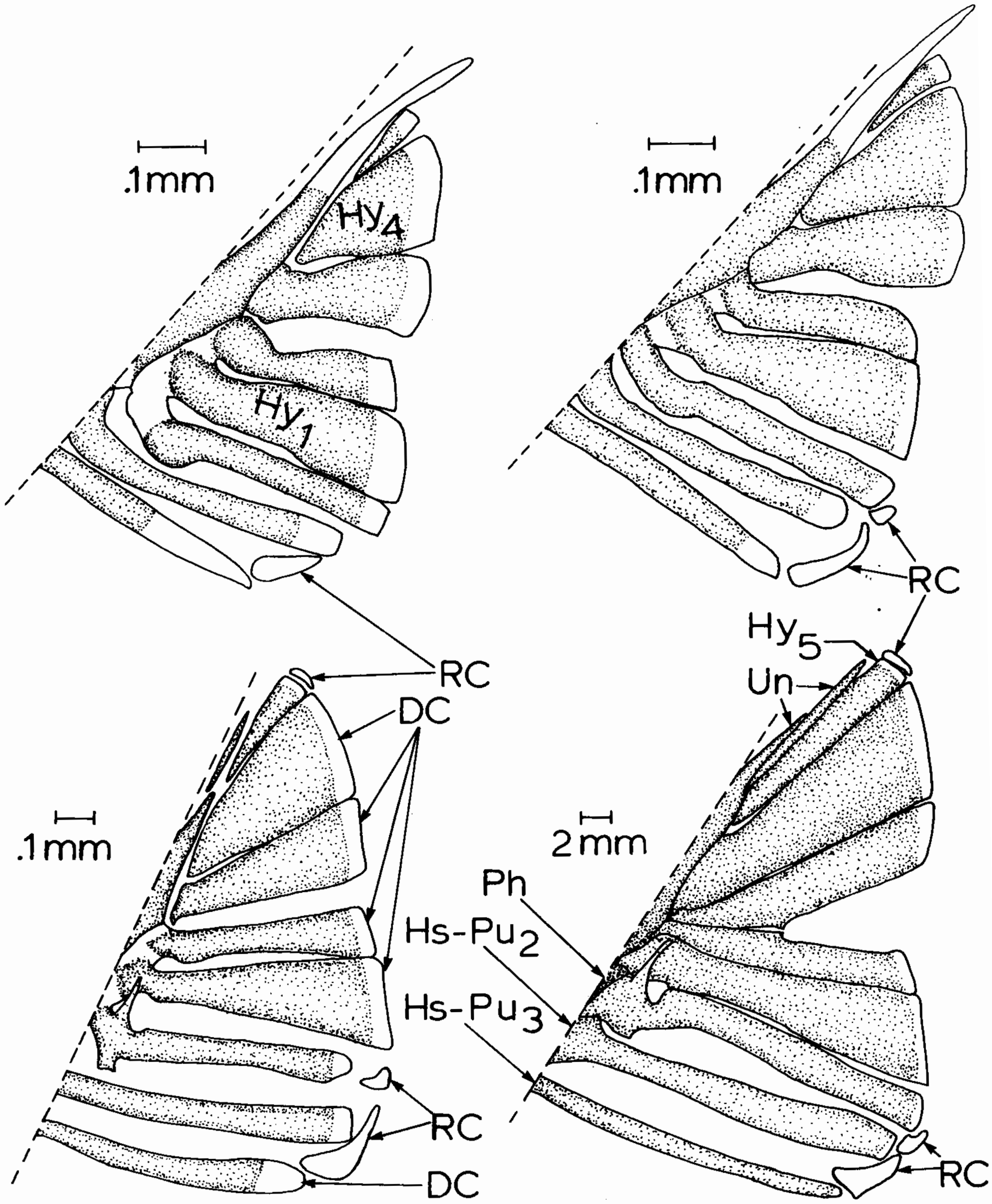

Figure 7. Development of the radial cartilages in relation to hypural bones and haemal spines in *Lutjanus campechanus*. Top left to bottom right specimens' lengths in mm SL are: 6.5, 7.2, 13.0, 300. DC, distal cartilage. For other abbreviations, see Figure 6.

velops shortly before posttemporal at 2.9 or 3.0 mm NL, posttemporal between 2.9 and 3.6 mm NL. Large spines develop on supratemporal and posttemporal bones; spines become serrations in juveniles and disappear in adults. Two postcleithra also bones of dermal origin. Long rod-shaped ventral postcleithrum develops first between 3.0 and 3.7 mm NL, followed by short rod-shaped dorsal postcleithrum between 3.7 and 4.2 mm NL or SL. During ontogeny rod-shaped

Table 5. Cartilage development and ossification of the caudal complex in *Lutjanus campechanus* (PU, preural centrum)

	Range (mm NL or SL) of appearance in cartilage	Range (mm NL or SL) of ossification
PU_3—Centrum	—	5.6–6.3
PU_3—Neural spine	3.6–4.2	6.5–7.9
PU_2—Centrum	—	5.6–6.4
PU_2—Specialized neural arch	3.6–4.2	7.1–9.5
Epural—anterior	3.9–4.6	>9.5 < 13.0
middle	3.9–4.6	>9.5 < 13.0
posterior	4.0–4.7	>9.5 < 13.0
Uroneural—anterior	—	5.3–8.3
posterior	—	>9.5 < 13.0
Hypural 5	4.6–5.8	5.9–9.5
Hypural 4	3.7–4.2	4.8–6.5
Hypural 3	3.6–4.2	4.8–6.5
Hypural 2	3.6–4.2	4.8–6.5
Hypural 1	3.6–4.2	4.8–6.5
Parhypural	3.6–4.2	5.1–7.9
Urostyle	—	4.8–6.4
PU_2—Haemal spine	3.6–4.2	6.6–7.9
PU_3—Haemal spine	3.6–4.2	6.4–7.9
Anterior ventral radial cartilage	5.9–6.5	—
Posterior ventral radial cartilage	7.2–9.1	—
Hypural 5 radial cartilage	>9.5 < 13.0	—

postcleithra acquire large shelves and become broad bones in adults. Two supratemporal-intertemporal bones of dermal origin and develop last in pectoral-fin suspensorium; they develop between 13.0 and 21.0 mm SL, size range with no specimens available.

Pelvic Fin and Supports (Figs. 8, 9, 10, Tables 2, 6).—Adult pelvic fin ray count I,5. Fin spine develops first on lateral side of basipterygium in specimens between 3.4 and 3.9 mm NL. Pelvic fin rays added from lateral to medial and adult counts attained between 4.3 and 5.0 mm SL. The 5.4-mm SL specimen represents exception with count of I,4 in both fins. Pelvic fin spines develop fine serrations on lateral edge between 4.6 and 5.6 mm SL. Serrations present in 13.0 mm SL specimen, but absent in specimens 21.0 mm SL and larger.

Pelvic fins supported by two basipterygia, characterized by three wings stemming from central part. Dorsad internal and external wing, and ventrad ventral wing. Posteriorly at base of fin ray articulation large posterior xiphoid process and small anterior xiphoid process. Cartilaginous basipterygia first develop between 3.0 and 3.6 mm NL, their anterior tips extending between cleithra. Signs of basipterygia ossification observed first in specimens between 3.6 and 4.3 mm NL or SL. Further development consists of addition of three wings and xiphoid processes.

Spinous Dorsal Fin (Figs. 1, 11–13, Table 2).—Specimens 7.2 mm SL and larger with 10 dorsal spines. Second and third dorsal spines first seen in one 3.1 mm NL specimen, and all larvae 3.6 mm NL or longer with two or more fin spines developing. Anteriormost spine develops after second, third and fourth anteriormost spines developed. Addition of fifth to tenth spines in a posterior direction, development of posteriormost 8 to 10 spines at first resembles soft ray development, because these spines with frayed tips, which become pointed. Complete

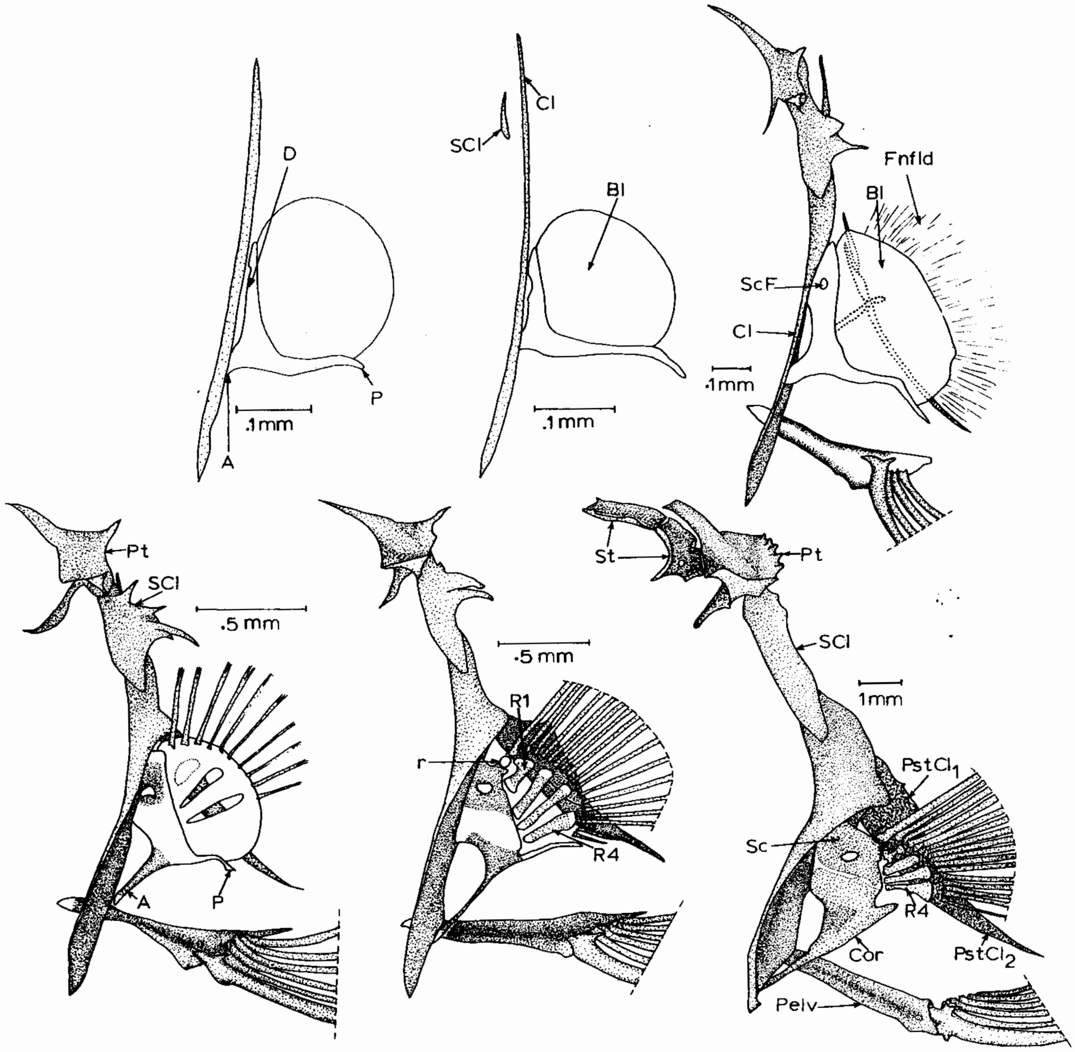

Figure 8. Development of the pectoral fin, pectoral girdle and suspensorium in *Lutjanus campechanus.* Top left to bottom right specimens' lengths in mm NL or SL are: 2.8, 2.9, 4.1, 6.6, 9.5, 37.4. A, anterior process of coracoid or coraco-scapular cartilage; Bl, cartilaginous pectoral fin blade; Cl, cleithrum; Cor, coracoid; D, dorsal process of coraco-scapular cartilage; Fnfld, finfold; P, posterior process of coracoid or coraco-scapular cartilage; Pelv, pelvic basipterygium; PstCl, postcleithrum; Pt, posttemporal; r, cartilaginous distal radial; R, proximal radial; Sc, scapula; ScF, scapular foramen; SCl, supracleithrum; St, supratemporal-intertemporal. Cartilage white; ossifying, stippled.

spinous dorsal fin count of VIII,2 or IX,1 or X first observed at 4.0 mm NL and all specimens 4.9 mm SL and larger have complete count. Each dorsal spine in juveniles and adults with foramen in its base. These foramina receive spinous hooks from distal radials. Dorsal spines smooth throughout development.

Spinous Dorsal Fin Supports (Figs. 1, 11–13, Table 1).—Adults with three predorsal bones anterior to dorsal fin pterygiophores. Anteriormost pterygiophore develops first in cartilage between 3.0 and 3.5 mm NL and addition of more cartilaginous pterygiophores in posterior direction. After four pterygiophores de-

Table 6. Development of the pelvic basipterygium and the bones in the pectoral girdle in *Lutjanus campechanus*

	Range (mm NL or SL) of appearance in cartilage	Range (mm NL or SL) of ossification
Cleithrum	—	<2.5–2.5
Blade	<2.5–2.5	—
Coraco-scapular cartilage	<2.5–2.5	—
Scapular foramen	3.6–4.0	—
Scapula	—	5.0–6.2
Coracoid	—	4.8–6.2
Blade cleavage, dorsal	4.0–4.5	—
central	3.8–4.2	—
ventral	5.0–7.1	—
Proximal radials	7.1*	9.1–13.0
Distal radials, dorsalmost	7.2	—
ventralmost	>9.5 < 13.0	—
Supratemporal–intertemporal	—	>13.0 < 21.0
Posttemporal	—	2.9–3.6
Supracleithrum	—	2.9–3.0
Postcleithrum, dorsal	—	3.7–4.2
ventral	—	3.0–3.7
Pelvic basipterygium	3.0–3.6	3.6–4.3

* In specimens 5.4–6.9 mm SL, pectoral blades were damaged or in poor condition.

velop, three predorsal bones appear simultaneously in cartilage between 3.1 and 3.6 mm NL; fin spines appear after two pterygiophores develop. Full complement of eight spinous dorsal-fin pterygiophores attained between 3.6 and 3.8 mm NL. Ossification begins with anteriormost proximal radial between 3.6 and 4.0 mm NL or SL and proceeds in posterior direction. All spinous dorsal-fin proximal radials ossifying in specimens 7.1 mm SL and larger. Ossification of distal radials occurs after onset of ossification of respective proximal radial. Predorsals begin to ossify after proximal radial ossification onset, between 4.4 and 7.1 mm SL. Ossification of three predorsals simultaneous, except in one 4.8-mm SL specimen in which only anteriormost predorsal ossifying.

Each pterygiophore and each predorsal bone originate from one piece of cartilage. Although anteriormost pterygiophore more massive and dorsally more expanded, we did not observe two pieces of cartilage or cartilaginous fusion in first pterygiophore during any part of ontogeny. After fin-spine formation, distal cartilage separates from proximal cartilage near base of fin spine. In juveniles separate distal radials begin to fuse with their respective proximal radials and all distal radials of spinous dorsal fin fused to proximal radials, in adults. Each pterygiophore supports one fin spine in serial association (e.g., proximal radial, distal radial, fin spine). Anteriormost pterygiophore in addition supports two supernumerary spines, which lack distal radials, but attached to proximal radial by ring of bone. All spinous-dorsal fin pterygiophores develop two lateral and two sagittal keels on proximal radials after initial ossification.

Soft Dorsal Fin (Figs. 13–15, Table 2).—Juveniles and adults with 13 to 15 soft dorsal-fin rays. Of 31 specimens two have 13, 28 have 14, and one has 15 rays. Soft dorsal-fin rays are first seen at anterior portion of soft dorsal fin, directly posterior to spinous dorsal fin, in specimens between 4.0 and 4.8 mm NL having complete complements of dorsal spines. Addition of fin rays caudad. Complete counts first observed in specimens between 4.8 and 5.8 mm SL. Soft dorsal-fin rays have bifurcated bases, which hold serially associated distal radials.

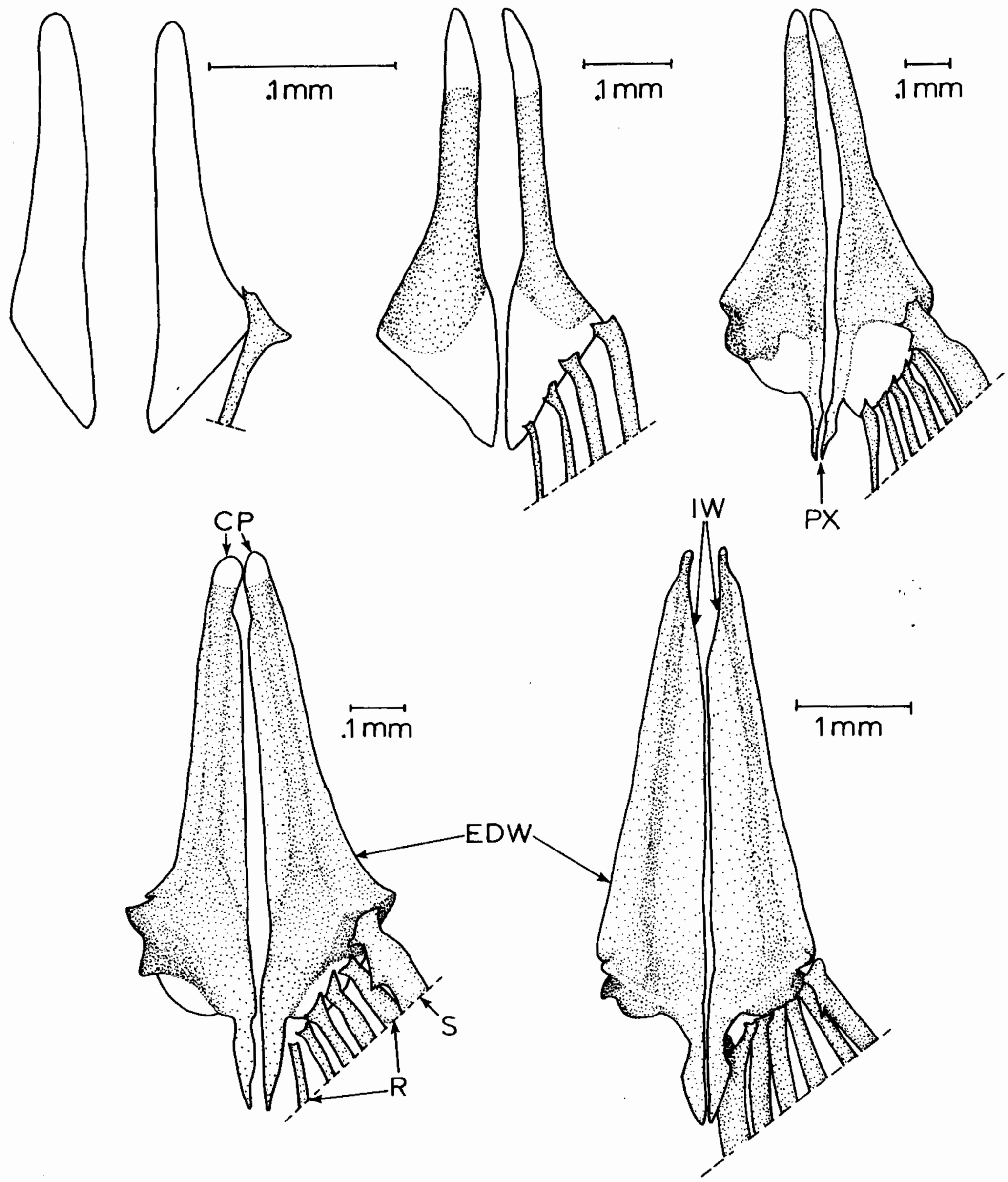

Figure 9. Development of pelvic basipterygia in *Lutjanus campechanus,* dorsal view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.4, 3.5, 5.7, 5.9, 28.3. CP, central part; EDW, external dorsolateral wing; IW, internal wing; PX, posterior xiphoid process; R, fin ray; S, fin spine. Cartilage, white; ossifying, stippled.

Soft Dorsal Fin Supports (Figs. 13–15, Table 1).—Most frequently with 14 soft dorsal-fin pterygiophores. Soft dorsal-fin pterygiophores have proximal and distal radials. Posteriormost three to five pterygiophores also with middle radial and posteriormost pterygiophore with crescent-shaped stay. Anteriormost soft dorsal-fin pterygiophores first to develop in larvae 3.7 and 3.8 mm NL, following posteriormost spinous dorsal-fin pterygiophores in sequence. Addition of pterygiophores in posterior direction and full complement attained between 4.1 and 5.1

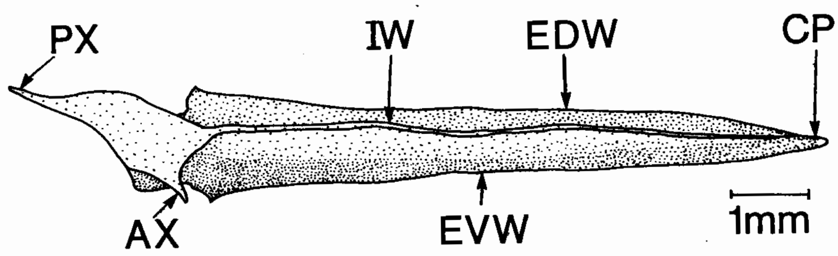

Figure 10. Internal view of left basipterygium in a 56-mm SL *Lutjanus campechanus*. AX, anterior xiphoid process; EVW, external ventrolateral wing. For other abbreviations, see Figure 9.

mm SL. Ossification of soft dorsal-fin pterygiophores (proximal radials) starts anteriorly at 7.1 mm SL, and proceeds posteriorly. Complement complete between 13.0 and 21.0 mm SL, size range with no specimens available. Distal radials ossify after ossification onset of respective proximal radials.

Each soft dorsal-fin pterygiophore, including posteriormost pterygiophore and stay, develops from one piece of cartilage. Then fin ray forms at distal portion of cartilage with its bifurcated base gripping cartilage laterally. Afterwards distal portion of cartilage separates giving rise to distal and proximal radials. Middle radials in posterior pterygiophores do not separate from proximal radials in cartilaginous state, but ossify separately. After proximal radial ossification onset, small lateral and sagittal keels develop. Spherical distal radial cartilages located between fin-ray bases ossify bilaterally to two pieces of bone ventrally tipped by cartilage. Posteriormost pterygiophore supports double fin ray, with middle radial with ventral stay. Stay originates from pterygiophore cartilage. In juveniles middle radial ossifies dorsad and crescent-shaped bone ossifies ventrad in pterygiophore cartilage. Broad band of cartilage surrounds crescent stay ventrad in juveniles and adults.

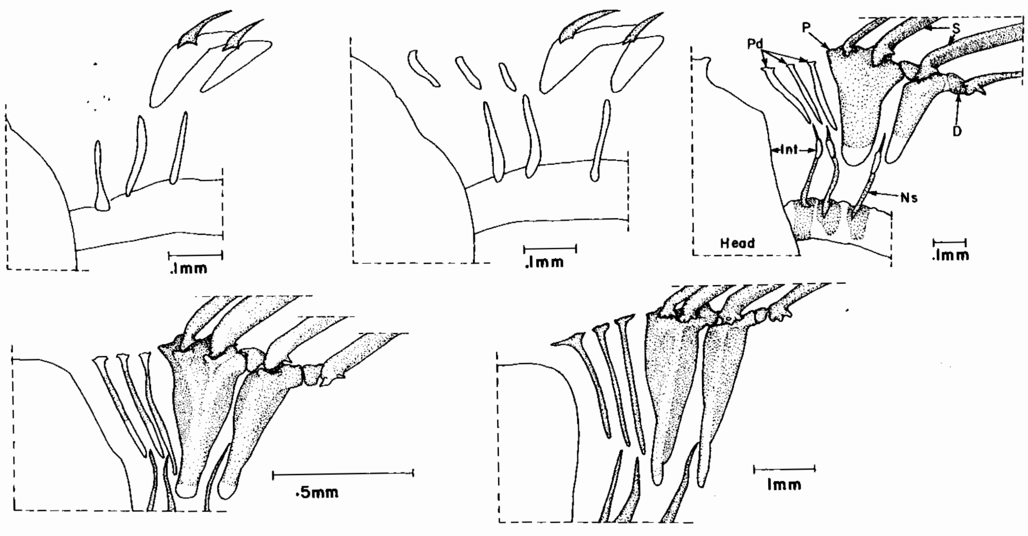

Figure 11. Development of predorsal bones, first two pterygiophores with associated fin spines and the relationship of these predorsals and pterygiophores to the first three interneural spaces in *Lutjanus campechanus*, left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.1, 3.1, 4.1, 6.6, 28.3. D, distal radial; Int, interneural space; Ns, neural spine; P, proximal radial; Pd, predorsal bone; S, fin spine. Cartilage, white; ossifying, stippled.

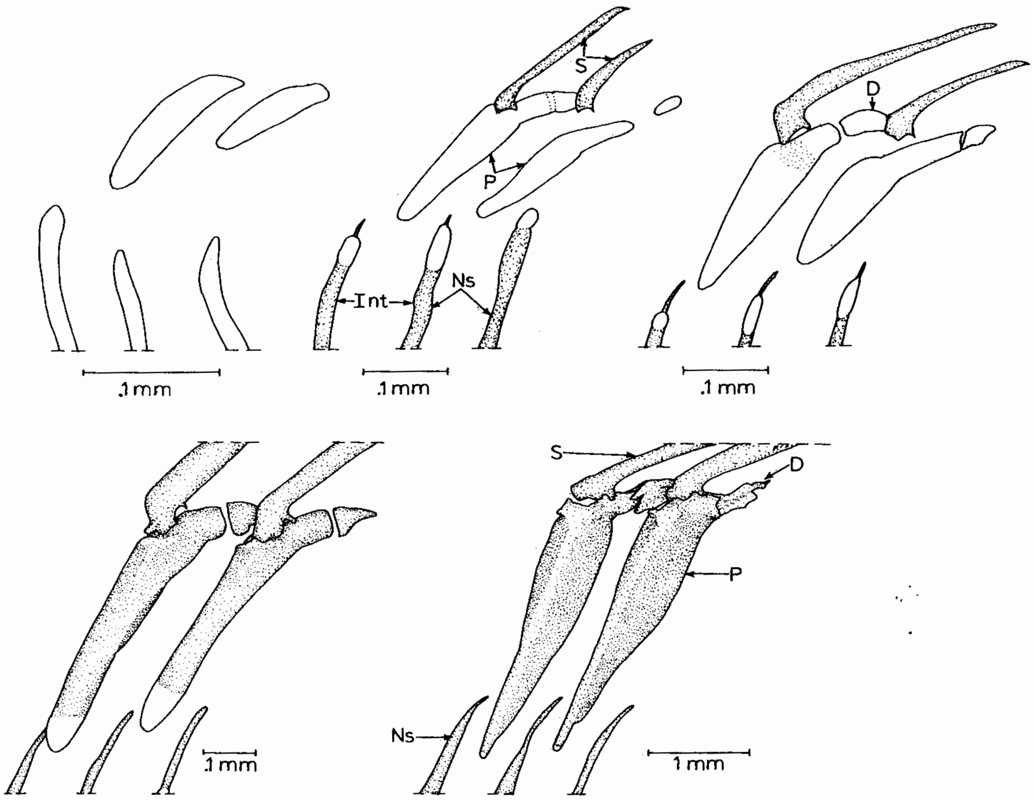

Figure 12. Development of 4th and 5th spinous dorsal-fin pterygiophores and their relationship to the 4th, 5th and 6th neural spines in *Lutjanus campechanus,* left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.5, 3.9, 4.1, 6.6, 28.3. For abbreviations, see Figure 11. Cartilage, white; ossifying, stippled.

Anal Fin (Figs. 13, 16, Table 2).—Anal fin spine and ray count of III,9 (rarely III,8). Two specimens with III,8 count also with low and uncommon count of 13 soft dorsal-fin rays. Anal fin spines and rays start to develop anteriorly concurrent with completion of spinous dorsal fin and initial development of soft dorsal fin between 4.0 and 4.8 mm NL. All three anal spines start ontogeny as rays with frayed tips and later convert to spines, and third spine develops as ray over greatest size range. Second spine develops first, and only after addition of three or four rays in posterior direction does first anteriormost spine develop. Anal fin complete concurrent with soft dorsal fin in specimens between 4.8 and 5.8 mm SL. In this size range third anterior fin element still soft ray except in 5.8 mm SL specimen, where transformed to spine.

Anal Fin Supports (Figs. 13, 16, Table 1).—Juvenile and adult most frequently with 10 anal fin pterygiophores. Only nine pterygiophores present in two specimens where total anal spine and ray count III,8. Most anal fin pterygiophores similar in structure and arrangement to soft dorsal-fin pterygiophores, except anteriormost first anal pterygiophore, which resembles anteriormost spinous dorsal-fin pterygiophore. First to develop in larvae 3.6 to 4.2 mm NL are anterior anal pterygiophores with addition in posterior direction. Full complement of anal pterygiophores first observed in specimens between 4.0 and 4.9 mm SL. Ossification of anal pterygiophores (proximal radials) starts anteriorly with anteriormost

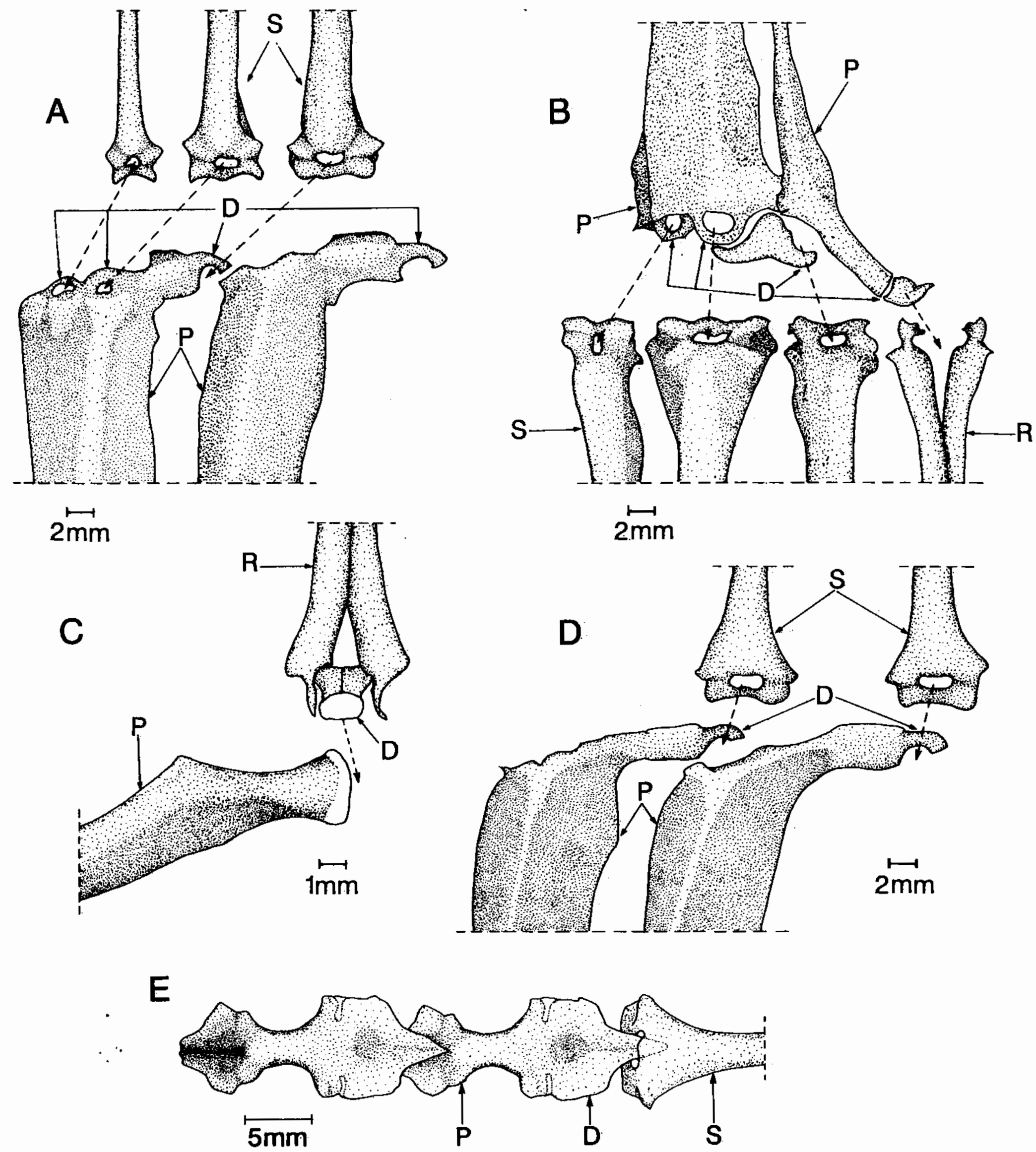

Figure 13. Selected pterygiophores and associated fin spines or soft rays from an adult *Lutjanus campechanus,* 332 mm SL. A, left lateral view of anteriormost two spinous dorsal-fin pterygiophores, associated spines were removed and the anterior views of the bases of the spines associated with the first pterygiophore are shown; B, left lateral view of first and second anal pterygiophores, associated spines and soft ray were removed and the anterior view of their bases is shown; C, left lateral view of posterior parts of 12th dorsal pterygiophore (4th from anterior in soft dorsal fin), serially associated ray was removed and anterior view of ray's base with distal radial is shown; D, left lateral view of 5th and 6th pterygiophores in spinous dorsal fin, serially associated soft rays were removed showing the anterior view of their bases; E, dorsal view of 5th and 6th pterygiophores in spinous dorsal fin with serially associated spine in place on 6th pterygiophore but removed on 5th. R, soft ray. For other abbreviations, see Figure 11. Cartilage, white; bone, stippled.

first anal pterygiophore in some specimens between 4.6 and 5.7 mm SL. Ossification proceeds in posterior direction and complete between 13.0 and 21.0 mm SL, size range for which no specimens available. Distal radials ossify after respective proximal radials.

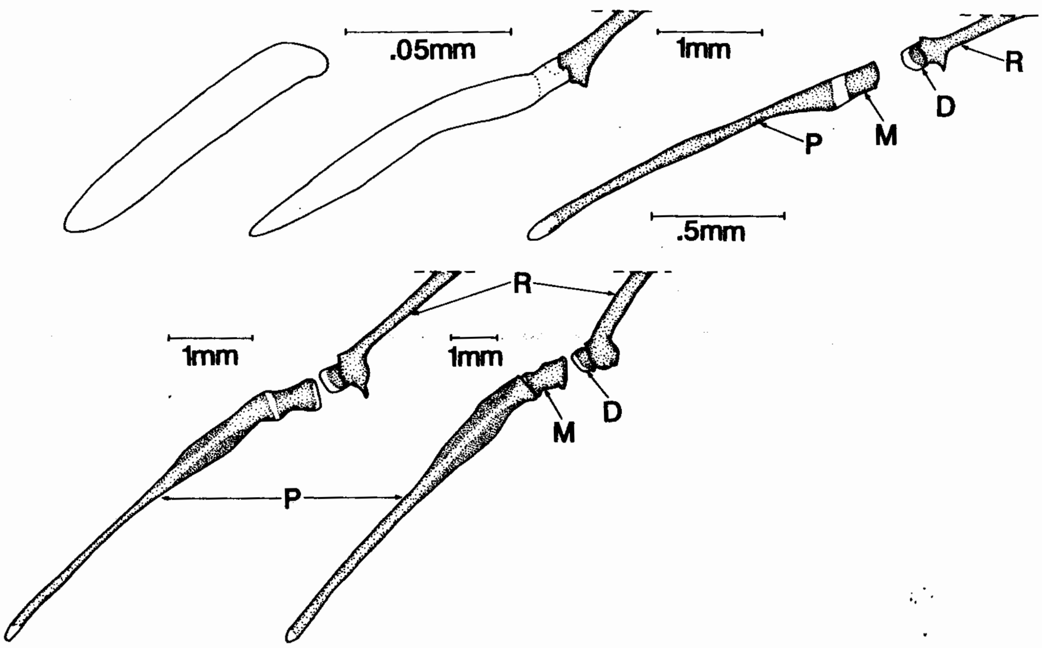

Figure 14. Development of the 20th dorsal pterygiophore (12th of the soft dorsal fin) and its serially associated fin ray in *Lutjanus campechanus*, left lateral view. Top left to bottom right specimens' lengths in mm SL are: 4.7, 6.6, 28.3, 70, 120. M, middle radial. For other abbreviations, see Figures 11 and 13. Cartilage, white; ossifying, stippled.

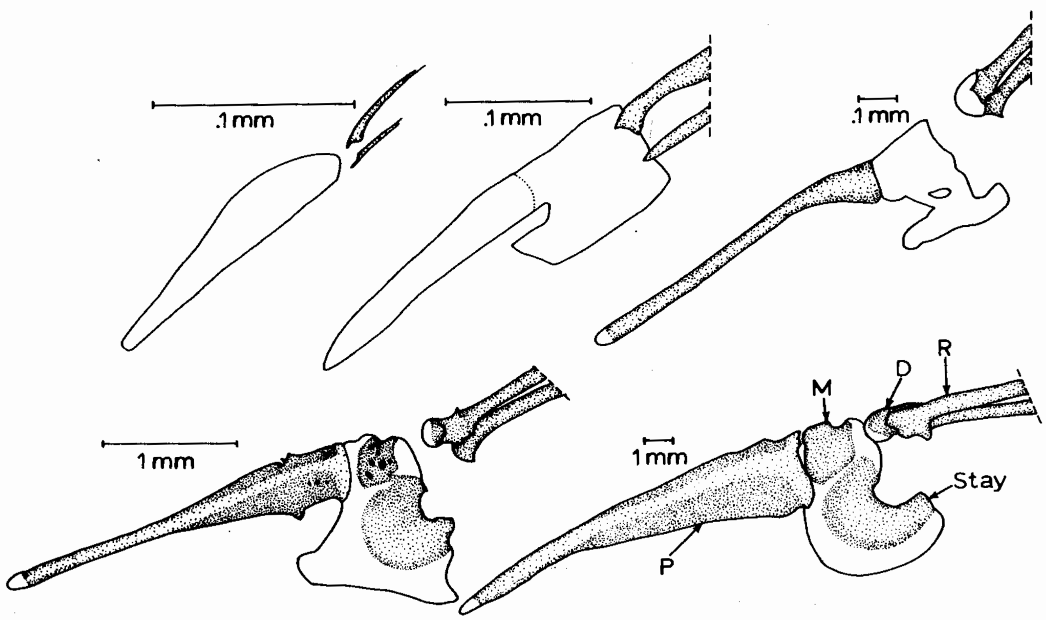

Figure 15. Development of posteriormost soft dorsal fin pterygiophore and its serially associated double fin ray and stay in *Lutjanus campechanus*, left lateral view. Top left to bottom right specimens' lengths in mm SL are: 5.3, 6.6, 28.3, 70, 332. For abbreviations, see Figures 11 and 13. Cartilage, white; ossifying, stippled.

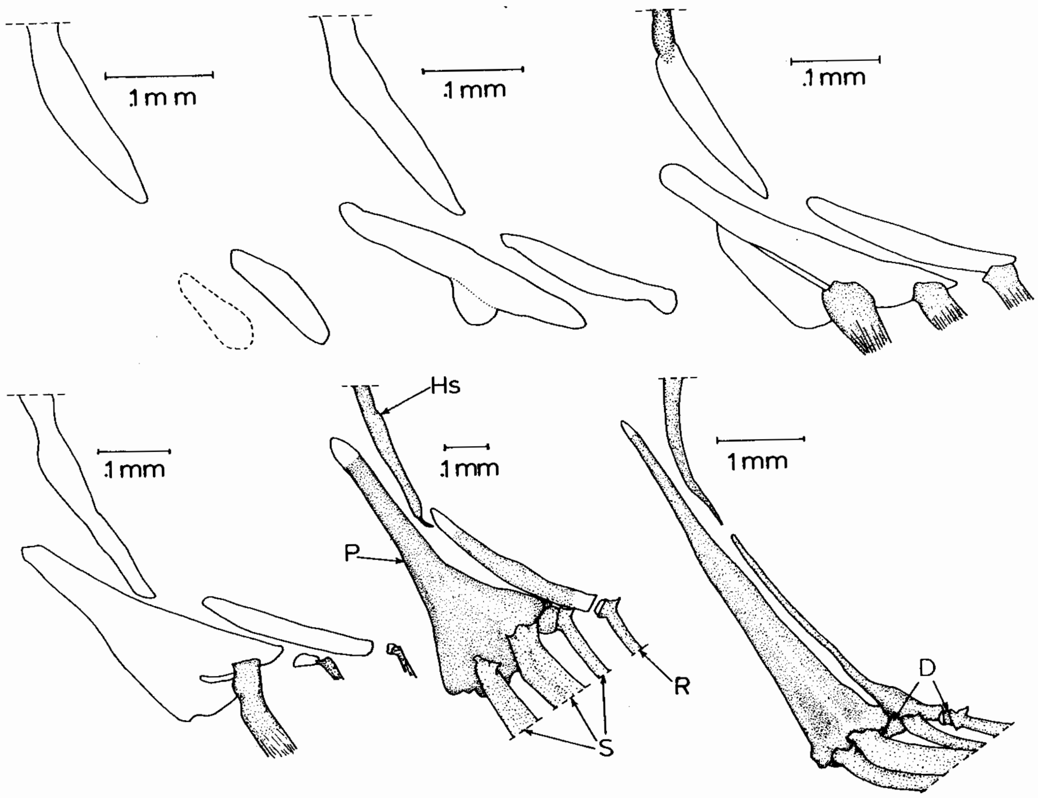

Figure 16. Development of the anteriormost two anal pterygiophores and their fin spines and rays, showing the relationship to the first haemal spine, left lateral view. Top left to bottom right specimens' lengths in mm NL or SL are: 3.9, 4.1, 4.5, 4.8, 6.5, 28.3. Hs, haemal spine. For other abbreviations, see Figures 11 and 13. Cartilage, white; ossifying, stippled.

Individual anal fin pterygiophores develop similar to soft dorsal-fin pterygiophores. As in soft dorsal fin, three to five middle radials and stay are present in anal fin supports. Usually one less middle radial in anal fin supports than in soft dorsal fin supports. Anteriormost anal pterygiophore exceptionally develops from two pieces of cartilage, which fuse. Two supernumerary spines attached by rings of bone similar to anteriormost spinous dorsal-fin pterygiophore, but serially associated spine articulates to free distal radial by radial's hook through spine's foramen.

Fin Spine and Ray Association with Pterygiophores, Arrangement of Predorsal Bones and Pterygiophores in the Interneural and Interhaemal Spaces (Figs. 1, 11–17).—Anteriorly three predorsal bones, which do not support fin spines. First dorsal pterygiophore supports three spines. First and second spines supernumerary, and third spine serially associated with first pterygiophore, remaining dorsal-fin pterygiophores with one serially associated spine or ray (e.g., proximal radial, distal radial, fin spine or ray) and secondarily associated spine or ray present anteriorly on proximal radial. This secondarily associated spine or ray serially associated with anteriorly preceding pterygiophore. Only posteriormost dorsal double fin ray with no secondary association. Anal fin ray association same as in soft dorsal fin. Anal fin spines associate with first anal pterygiophore same way as dorsal spines with anteriormost dorsal pterygiophore, except anteriormost anal pterygiophore with free distal radial.

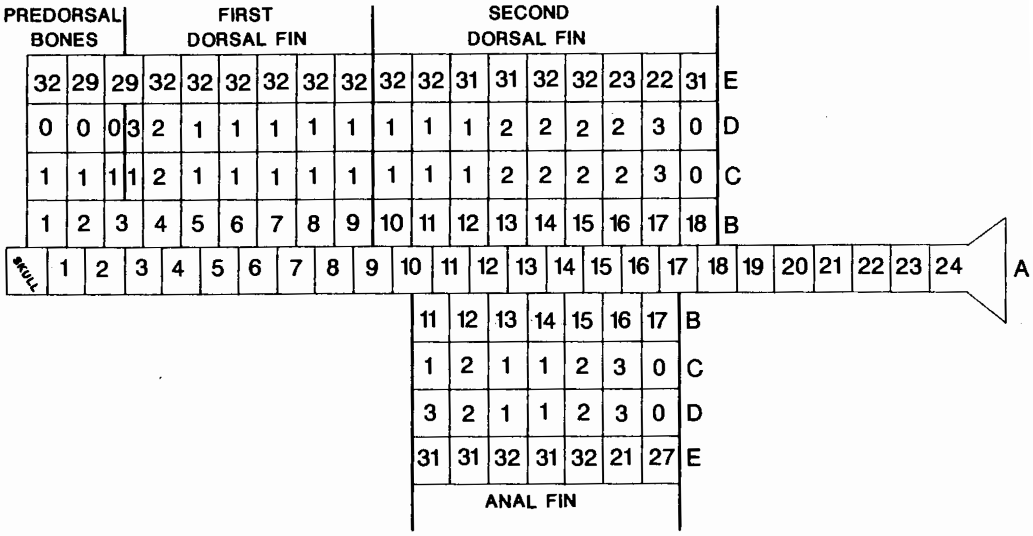

Figure 17. Common arrangement of predorsal bones, pterygiophores, fin spines and soft rays in relation to the skull and vertebral column for 32 *Lutjanus campechanus* (4.8–332 mm SL). Modified after Matsui (1967). A, skull and vertebra numbers; B, interneural and interhaemal space numbers; C, number of predorsal bones or pterygiophores inserting in the respective interneural or interhaemal space; D, number of fin spines or soft rays serially associated with the respective pterygiophores; E, frequency of occurrence in 32 specimens for number of pterygiophores in respective interneural or interhaemal spaces.

Interneural and interhaemal spaces delineated by neural and haemal spines, except first interneural space anteriorly bound by skull and first interhaemal space by gut. In Figure 17 interhaemal spaces numbered same as opposing interneural spaces; therefore, first interhaemal space number 12. Pterygiophore insertion pattern (Fig. 17) into interneural and interhaemal spaces constant in 32 specimens for anteriormost predorsal bone. Pattern shown for second and third predorsals occurs only in 29 out of 32 specimens. Insertion pattern for spinous dorsal-fin pterygiophores constant and almost constant for first nine soft dorsal pterygiophores, but variable for last five. Dorsal fin supports terminate 31 times in 32 specimens in interneural space number 17 and once in number 18. Most commonly (22 of 32) three pterygiophores insert into space number 17. Insertion pattern almost constant for first nine pterygiophores above anal fin. Variability only for interhaemal spaces 16 and 17. Last anal fin supports most often insert into space 16 (27 of 32, not shown in Fig. 17) and 21 specimens with three pterygiophores inserting into interhaemal space 16. Interhaemal space 17 with one pterygiophore in five specimens and no pterygiophores in 27.

Branchiostegal Rays and Hyoid Arch (Fig. 18, Table 3).—Seven branchiostegal rays on each side, directly and indirectly supported by bones of hyoid arch. Posteriorly, small interhyal bone connects hyoid arch to hyomandibular bone. Interhyal connects ventrally with epihyal, which in turn partially fused with ceratohyal. Epihyal and ceratohyal directly support branchiostegal rays. Two rays articulate on epihyal and five on ceratohyal. Anteriorly, adjacent to ceratohyal bone, dorsal and ventral hypohyals connect hyoid arch anteriorly to basibranchial 1 of branchial skeleton.

Branchiostegal rays only bones of dermal origin in hyoid arch. Posteriormost ray first observed in larvae 2.8 mm NL. Addition of branchiostegals in anterior

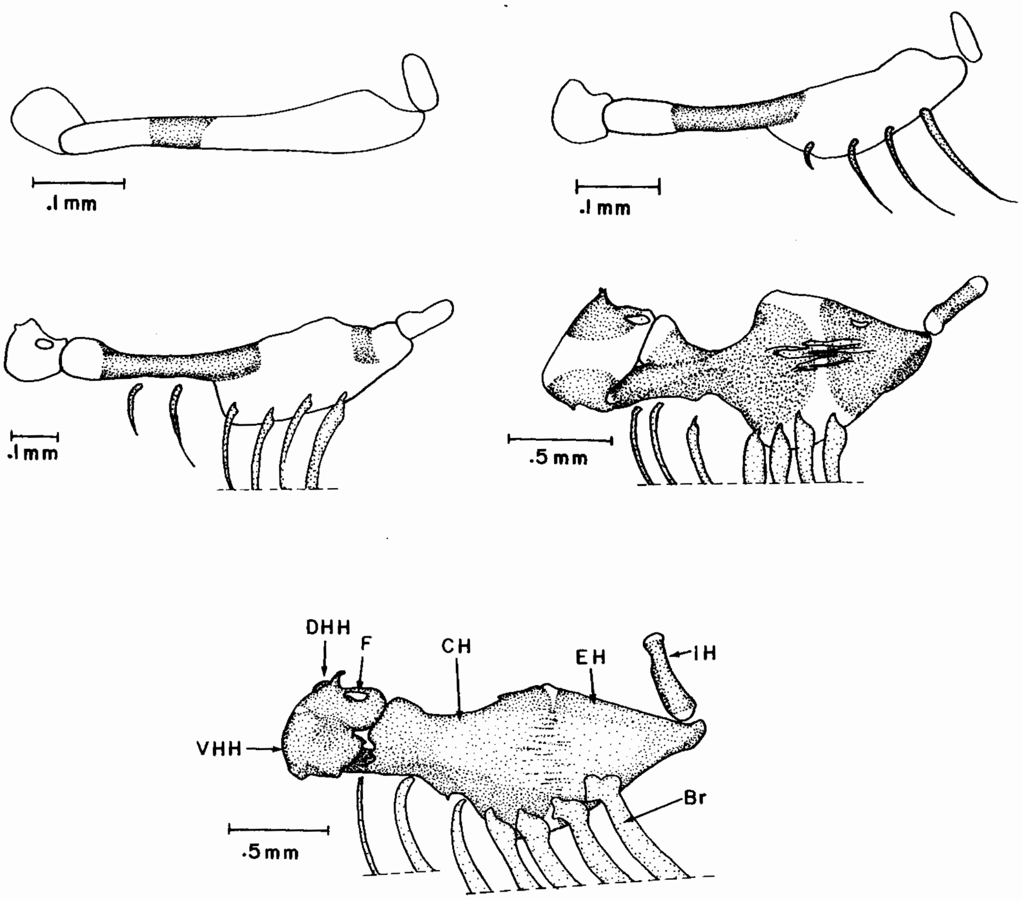

Figure 18. Development of the left hyoid arch with its branchiostegal rays in *Lutjanus campechanus*, left lateral view. Top left to bottom center specimens' lengths in mm NL or SL are: 2.5, 3.2, 3.6, 13.0, 120. Br, branchiostegal ray; CH, ceratohyal; DHH, dorsal hypohyal; EH, epihyal; F, foramen in dorsal hypohyal; IH, interhyal; VHH, ventral hypohyal. Cartilage, white; ossifying, stippled.

direction. Usually equal number of branchiostegals developing on each side. Only two specimens in 56 differed by one ray for both sides. Full count of seven rays attained between 3.7 and 4.5 mm NL or SL.

Hyoid arch present in our smallest 2.5 mm NL specimen and consists of three cartilages: interhyal, epi-ceratohyal, and hypohyal. Interhyal cartilage ossifies to one interhyal bone. Epi-ceratohyal cartilage with two ossification loci, which ossify to the epihyal and ceratohyal bones. In juveniles these two bones separated by cartilage, but bridged in center by bone. In adults epihyal and ceratohyal fused. Hypohyal cartilage acquires a foramen dorsad. The two ossifications appear dorsad and ventrad in cartilage. Ossifications spread and become dorsal and ventral hypohyal bones. Foramen of hypohyal cartilage retained in dorsal hypohyal bone.

Branchial Skeleton (Figs. 19, 20, Table 3).—Brachial skeleton with upper and lower portion. Lower branchial skeleton with five arches. First three arches with ceratobranchial and hypobranchial bone on each side with basibranchial in middle. Fourth lower arch consists of two ceratobranchials with cartilaginous basibranchial in center and fifth arch reduced to two ceratobranchials. First three arches with two rows (outer and inner) of gillrakers or toothpatches extending

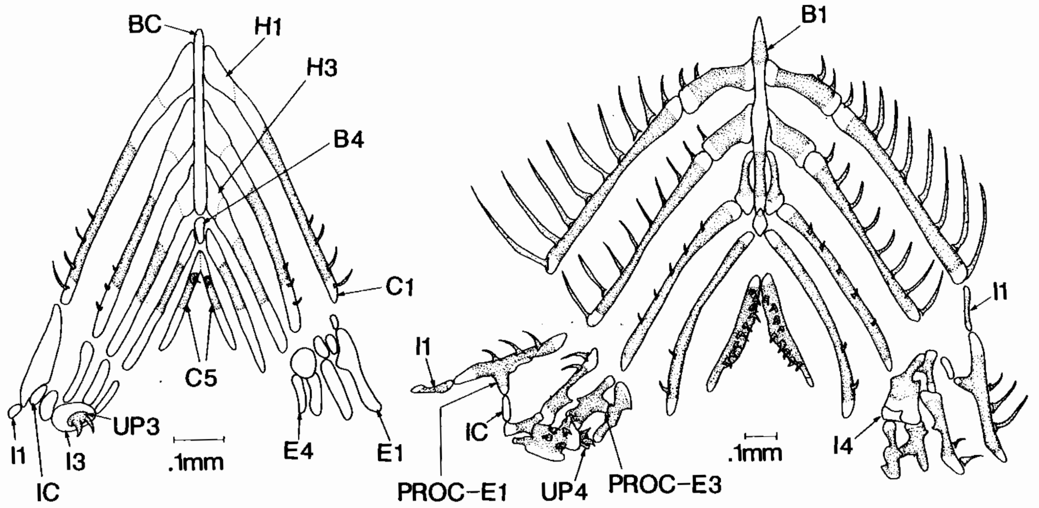

Figure 19. Development of the branchial skeleton in *Lutjanus campechanus,* dorsal view for lower arches (toward top of page), ventral view for left upper arches and dorsal view for right upper arches (toward bottom of page). Upper arches are cut and are not in their natural positions. From left to right specimens' lengths in mm NL or SL are: 3.4, 6.6. B, basibranchial; BC, basibranchial cartilage of B1–3; C, ceratobranchial; E, epibranchial; H, hypobranchial; I, infrapharyngobranchial; IC, interarcual cartilage; PROC-E, process on epibranchial; UP, upper pharyngeal toothplate develops ventrad on infrapharyngobranchial. Cartilage, white; ossifying, stippled.

from ceratobranchials across hypobranchials to basibranchials. Fourth ceratobranchials also with two rows of toothpatches, but fifth ceratobranchials covered with non-autogenous (connected to endochondral bone) teeth almost over entire dorsal surfaces. Upper branchial skeleton only has four arches. Each arch consists of two bones, epibranchial and infrapharyngobranchial. Epibranchial 1 bears two rows (outer and inner) of gillrakers and toothpatches. Infrapharyngobranchial 1 without toothpatches and toothplates and suspends upper arches on both sides to skull. Epibranchial 1 connects to second arch from process through interarcual cartilage to infrapharyngobranchial 2. Epibranchial of second arch has two rows of toothpatches and bears large autogenous (not connected to endochondral bone) toothplate ventro-posteriorly. Second arch infrapharyngobranchial bears large non-autogenous (connected and fused to endochondral bone) toothplate ventrad. Third upper arch similar to second arch, except toothplate on epibranchial 3 non-autogenous (e.g., teeth part of epibranchial bone) and epibranchial 3 with large anterior process. Infrapharyngobranchial 3 has non-autogenous toothplate ventrad. Fourth upper arch has only one gillraker on epibranchial. Infrapharyngobranchial 4 has large non-autogenous toothplate ventrad.

Upper and lower branchial arches develop first from cartilage (endochondral). Gillrakers and toothpatches develop outside branchial cartilage (dermal). Origin of toothplates unclear. All toothplates seem part of endochondral bone (non-autogenous), except toothplate on epibranchial 2, which is autogenous, e.g., not attached to bone, and can be freely moved. All toothpatches in adults begin as gillrakers in larvae. Basibranchials 1–3 originate from one basibranchial cartilage. Basibranchial 4 originates from separate piece and never ossifies.

Only outer row gillrakers of first left arch counted in all specimens. Two gillrakers first seen at 3.0 mm NL on posterior portion of ceratobranchial. Addition of rakers in anterior direction. After three to five rakers present on ceratobranchial,

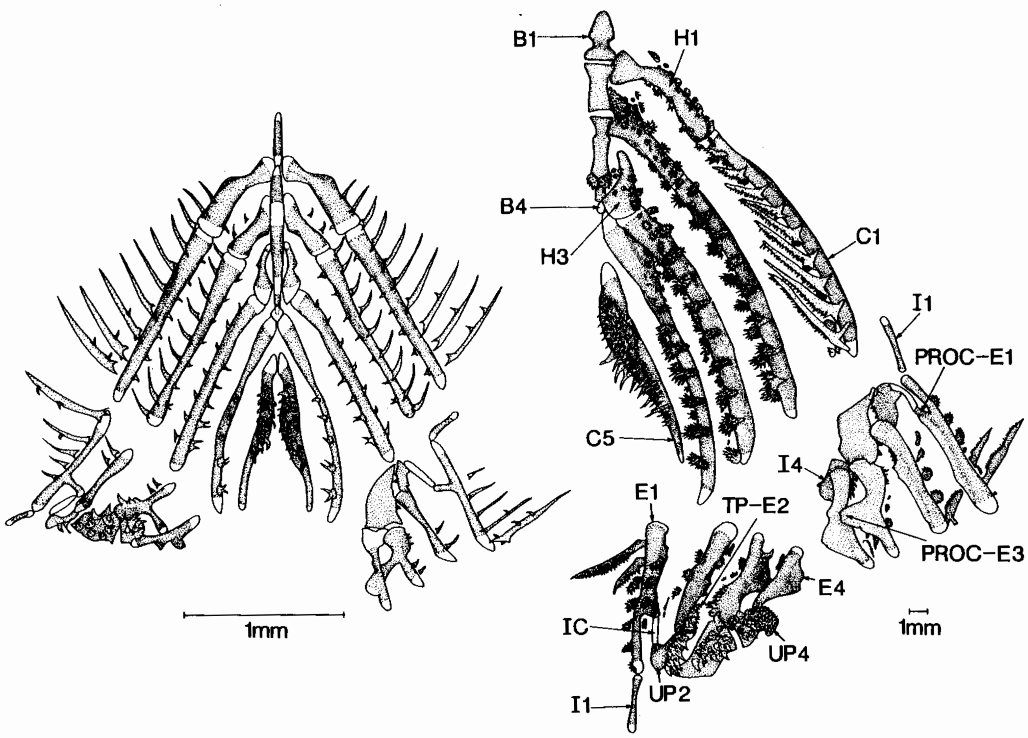

Figure 20. Development of the branchial skeleton in *Lutjanus campechanus,* dorsal view for lower arches (toward top of page), ventral view for left upper arches and dorsal view for right arches (toward bottom of page). Upper arches are cut and are not in their natural positions. Lower left arches have been removed for drawing on right. From left to right specimens' lengths in mm SL are: 13.0, 120. TP-E, toothplate of epibranchial. For other abbreviations, see Figure 19. Cartilage, white; ossifying, stippled.

raker in angle develops in sizes 3.4 to 3.9 mm NL. First raker on epibranchial develops in posterior corner near angle at 4.0 mm NL and additional rakers added anteriorly. Adult count of seven to eight rakers over ceratobranchial attained between 3.9 mm NL and 4.6 mm SL. Rakers over hypobranchial first observed at 4.8 mm SL and addition in anterior direction. Full hypobranchial count of five or six rakers attained between 28.3 and 37.4 mm SL. Of these rakers, one or two situated past hypobranchial anteriorly. Adult epibranchial count of six to eight rakers present in specimens 22.4 mm SL and larger. Total adult count for first arch left side outer gillrakers of 20 to 22 observed in all specimens 22.4 mm SL and larger.

All toothpatches on branchial skeleton of *L. campechanus* develop first as gillrakers. Most of these rakers gradually transform to toothpatches. Only rakers present in adults are outer rakers of first arch along ceratobranchial, in angle, and posterior portion of epibranchial. Outer rakers of first arch along hypobranchial and anterior part of epibranchial transformed to toothpatches during development. True rakers of first arch develop many fine teeth along interior edge, while exterior edge remains smooth.

Mandibular Arch (Figs. 21–23).—Mandibular arch comprised of upper and lower jaws. Upper jaw consists of two bones on each side: ventrally positioned premaxillary and dorsally located maxillary. In adults interior ventral surface of

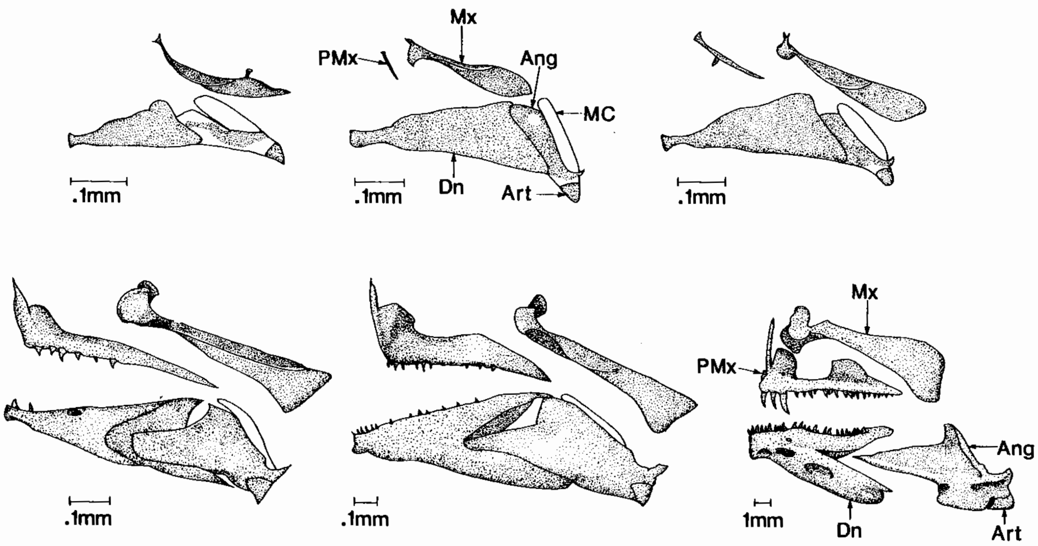

Figure 21. Development of the mandibular left arch in *Lutjanus campechanus*, left lateral view. The upper jaws in all drawings and the lower jaw in the bottom right side drawing are disarticulated to show the shape of the bones. Top left to bottom right specimens' lengths in mm NL or SL are: 2.9, 2.9, 3.1, 4.0, 7.1, 72. Ang, angular; Art, articular; Dn, dentary; MC, Meckel's cartilage; Mx, maxillary; PMx, premaxillary. Cartilage, white; ossifying, stippled.

premaxillary covered with slightly recurved conical teeth, and at ventral edge row of larger caniniform teeth with anteriormost four teeth being the largest. Three dorsal processes on the premaxillary. Anteriorly slender and long ascending process and next to it flat and broad process, which articulates between two flanges of maxillary's head. At posterior end of premaxillary another flat and broad dorsal process, which articulates with interior surface of maxillary. Slightly curved maxillary has no teeth, anteriorly two flanges fit over broad anterior process of premaxillary. Posteriorly maxillary greatly expanded. Part of this expansion projects over lower jaw. Lower jaw has three bones on each side. Anterior dentary, next angular bone and in posteriormost ventral corner of jaw is small articular bone, which in adults fused with angular. Dentary "V" shaped bone with angle of "V" forming tip of jaw. Dorsal arm of dentary has on its edge single row of caniniform teeth. At its anterior tip, interior to caniniform teeth, large patch of smaller cone-shaped slightly recurved teeth occurs. Angular bone has four processes. Anterior process triangular and fits between dorsal and ventral arms of dentary, long anterior dorsal process, and small posterior dorsal process. Angle formed by dorsal processes is articulatory fossa for quadrate bone. Ventral process broad rectangular shelf. Articular bone (also retroarticular) ontogenetically fused to angular and comprises ventro-posterior corner of angular's ventral process in adults. Meckel's cartilage, present in adults, found on interior surface on both sides of lower jaw, extends from anterior part of dentary's dorsal arm across anterior process of angular ventrally to articular and dorsally to angular's dorsal process.

In our smallest specimens (2.5 to 2.8 mm NL), only dermal maxillary present in upper jaw, no evidence of cartilaginous (endochondrous or epichondrous) ossification. Premaxillary first observed in one 2.9 mm NL specimen and present in all 3.0 mm NL specimens and larger, also dermal ossification and appears at first as sliver of bone curved around head of maxillary. Dorsal curvature develops into ascending process. First tooth seen on ventral edge of anterior portion of

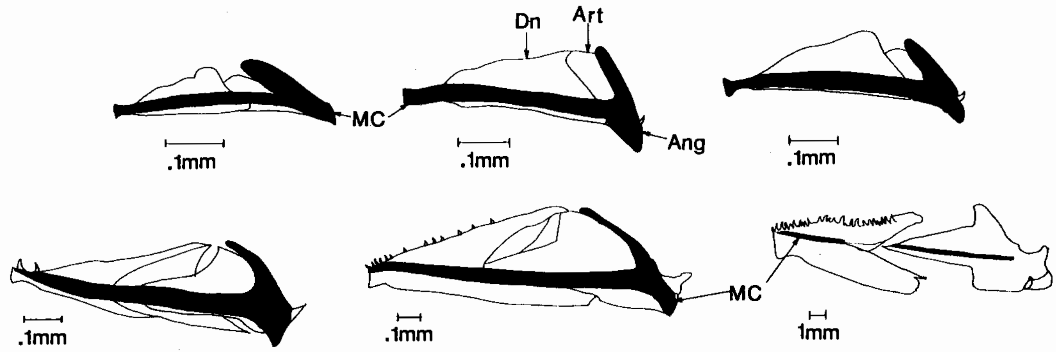

Figure 22. Development of Meckel's cartilage in relation to the bones of the lower left jaw in *Lutjanus campechanus*. The bones drawn in outline cover the cartilage drawn in black. For explanation of views, specimens' lengths and abbreviations, see Figure 21.

premaxillary in 3.1 mm NL larva and all specimens 3.5 mm NL and longer have one or more teeth on premaxillary. Maxillary and premaxillary bones change shape during ontogeny. In premaxillary it is primarily acquisition of teeth, the development of ascending and two broad dorsal processes. In maxillary it is primarily development of two flanges in head.

All components of lower jaw present in our smallest specimens 2.5–2.8 mm NL. In these specimens lower jaw consists of long piece of cartilage (Meckel's cartilage) with large dorsal process posteriorly. Epichondral ossification of dentary present extero-lateral and dorsal to ramus of jaw. At larger sizes endochondral ossification of dentary (Meckel's cartilage) at anterior portions occurs. At posteriormost ventral angle of jaw in our smallest specimens is articular endochondral ossification. Ossification of angular is endochondral and first seen at 2.9 mm NL posteriorly on lower jaw ramus. Ossification of angular also has epichondral element which grows to long dorsal process. Further ossification enlarges processes of dentary, angular, it enlarges angular fossa and fuses articular to angular.

Opercular Series (Figs. 24, 25, Table 3).—Opercular series comprises four dermal bones: preopercle, opercle, subopercle, and interopercle. Smallest 2.5 mm NL specimen has preopercle and opercle developed. Subopercle and interopercle develop in specimens between 2.9 and 3.5 mm NL. Subopercle ossifies before interopercle. Shape of four opercular bones changes during ontogeny, particularly shape of preopercular. On preopercular, larvae acquire up to six or seven large spines on interior shelf and three or four moderately sized spines on exterior shelf. In juveniles and adults interior shelf becomes serrated through addition of more and more spines with highest count of 128 spines (serrations) in adults. Spines on the exterior shelf become obtuse angles in late larvae and shelf smooth in juveniles. In adults, small sections of exterior shelf fuse to interior shelf, forming tunnel for latero-sensory canal.

Discussion

Developmental sequences, such as the locus of first appearance of neural and haemal arches and the subsequent direction of ontogenetic addition, have been little studied. These sequences may represent characters for determining familial, subordinal, and ordinal relationships. The first appearance and subsequent addition of neural and haemal arches in *L. campechanus* most closely resembles that of the scombroid *Istiophorus* (Potthoff et al., 1986) and the blennioid *En-*

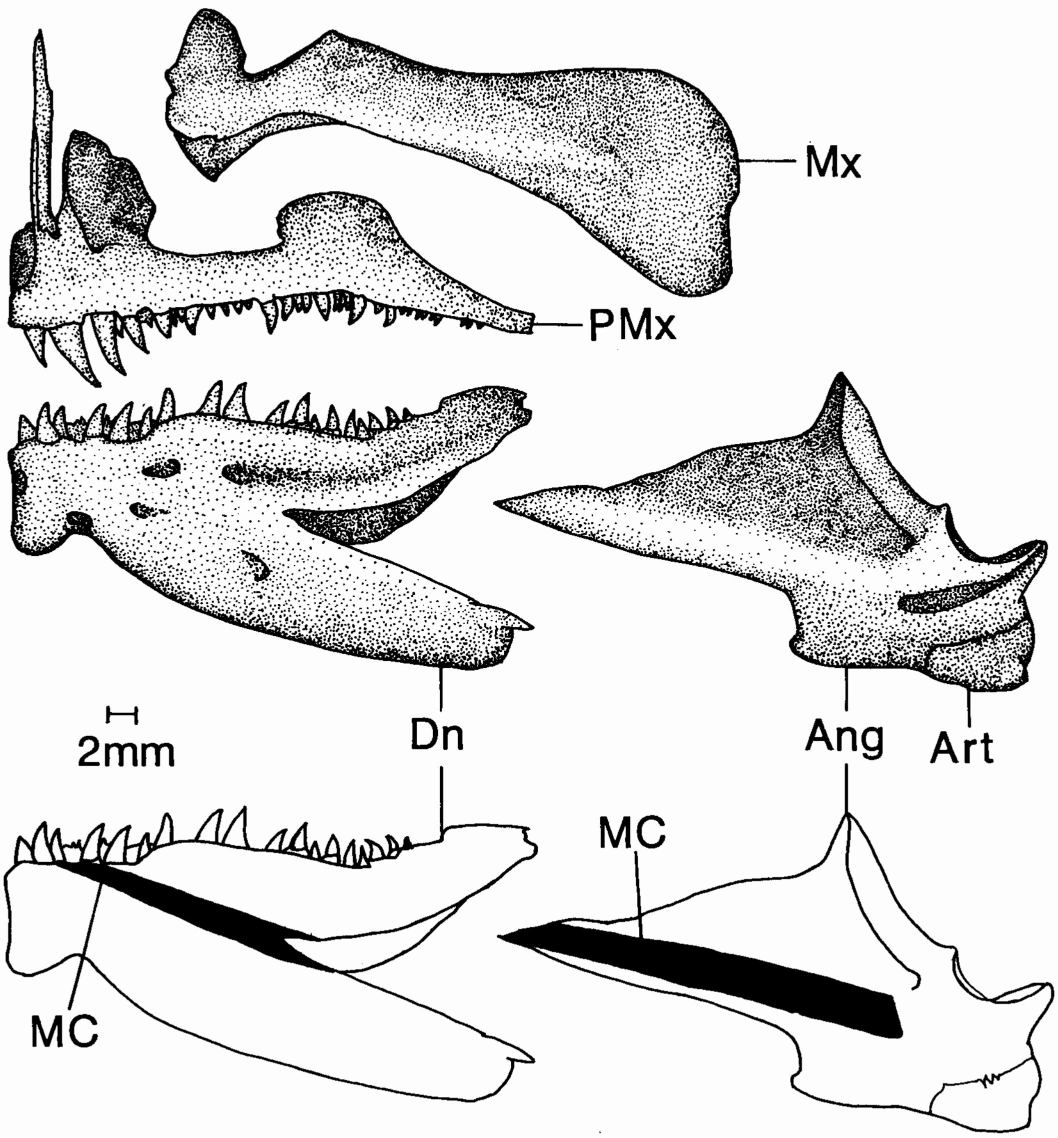

Figure 23. The left branchial arch of an adult *Lutjanus campechanus* 332 mm SL, left lateral view. The bones are disarticulated to show their shape. At the bottom is an outline drawing of the disarticulated lower jaw bones over Meckel's cartilage in black. For abbreviations, see Figure 21.

chelyurus brunneolus (Watson, 1987). Here the first appearance is in three places along the notochord (antero-dorsad, centro-ventrad, postero-ventrad). This was not observed in the percoid *Anisotremus virginicus*, where first appearance was in four places (antero-dorsad, centro-dorsad, centro-ventrad, postero-ventrad) (Potthoff et al., 1984). In the labroid *Microspathodon chrysurus*, Potthoff et al. (1987) assumed the first appearance was in four places because of gaps in the series studied. In *L. campechanus* ossification of the vertebral column (neural and haemal arches and spines, centra) starts anteriorly and proceeds posteriad. The urostyle and preural centra 2 and 3 ossify in an anterior direction. The same sequence of ossification was observed in a number of perciforms (Ahlstrom and Ball, 1954; Ahlstrom et al., 1976; discussion: Potthoff et al., 1987) and in a

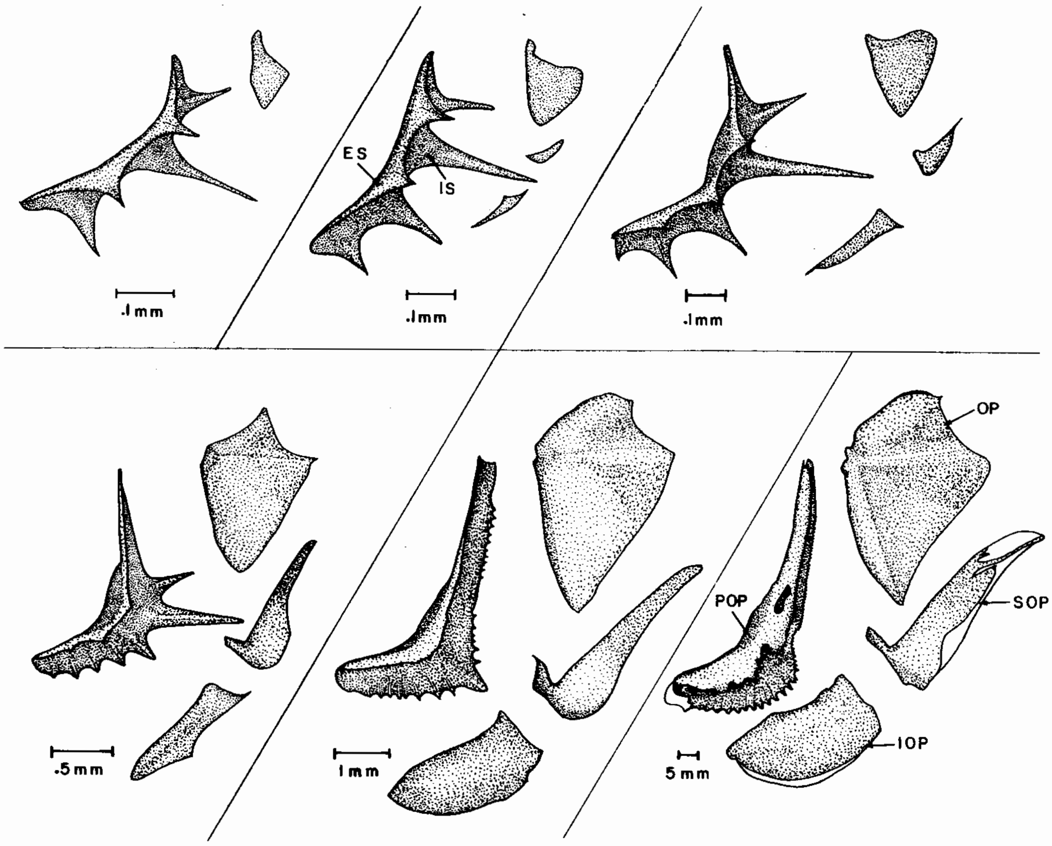

Figure 24. Development of the left opercular series in *Lutjanus campechanus,* lateral external view. Top left to bottom right specimens' lengths in mm NL or SL are: 2.5, 3.2, 3.6, 9.5, 22.4, 120. ES, external preopercular shelf; IOP, interopercle; IS, interior preopercular shelf; OP, opercle; POP, preopercle; SOP, subopercle. Hyaline blue stained area, white; red stained bone, stippled.

gadiform (Ahlstrom and Counts, 1955). In more primitive fish orders, sequence of ossification of the vertebral column seems to be entirely different. Nagięć (1977) reported a complicated sequence in the salmoniform *Coregonus larvaretus,* where ossification first starts posteriad with the hypural complex and proceeds anteriorly along the notochord, while a second ossification starts anteriorly and proceeds posteriorly. Houde et al. (1974) implied that in the clupeiform *Harengula jaguana* ossification of the vertebral column starts with the hypural complex, but they did not indicate subsequent direction of ossification. Richards et al. (1974) found that in the clupeiform *Opisthonema oglinum* the hypural complex starts to ossify first, then centra ossify from the middle of the column anteriorly and posteriorly, but neural and haemal spines ossify from posterior to anterior. Ahlstrom and Counts (1958) reported a complicated ossification sequence similar to *Opisthonema oglinum* in the stomiiform *Vinciguerria lucetia* in which the hypural complex starts to ossify first, followed by the centra in the center of the precaudal area. Centra ossification then proceeds anteriorly and posteriorly. In contrast, neural and haemal arches and spines ossify from posterior to anterior. Because ossification sequences for orders and suborders differ, it is reasonable to expect sequences of cartilage development to also differ and perhaps be useful in establishing relationships among higher taxa.

In *L. campechanus,* saddle-shaped ossifications appear dorsally and ventrally

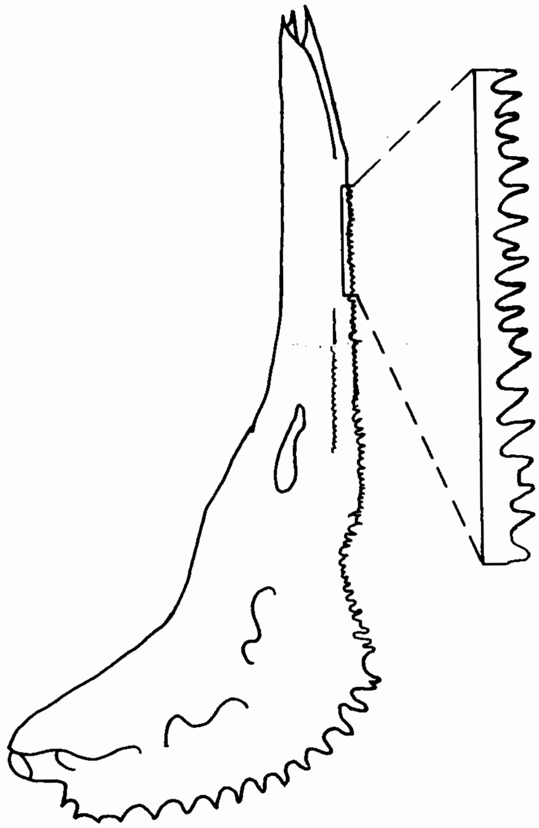

Figure 25. Outline drawing of the preopercle and an enlargement of part of the serrated edge of the interior shelf in a 120-mm SL *Lutjanus campechanus*.

when centra first ossify. Saddle-shaped ossifications do not occur in centra of all perciforms, such as in the primitive percoid *Morone* (Fritzsche and Johnson, 1980) and the scombroids Istiophoridae, Xiphiidae, Trichiuridae (Potthoff and Kelley, 1982; Potthoff et al., 1986), but are present in others such as Coryphaenidae (Potthoff, 1980), and Blenniidae (Watson, 1987), and the scombroids Scombrolabracidae, Gempylidae, Scombridae (Potthoff et al., 1986). Saddle-shaped ossifications have also been observed in more primitive fishes such as Clupeiformes (Richards et al., 1974) and Salmoniformes (Nagięć, 1977).

The arrangement of epipleural and pleural ribs in *L. campechanus* is typically percoid (Johnson, 1981), where eight pairs of pleural ribs are attached to precaudal centra 3 to 10 and eight pairs of epipleural ribs are associated with centra 1 to 8. Formation of ribs in a number of fish taxa has previously been discussed by Potthoff et al. (1984; 1987). Emel̆ianov (1935) gave a detailed account of rib development in fishes using histological techniques.

In *L. campechanus* the caudal fin is sequentially the third fin to start ray development (although it is almost concurrent with the pelvic fin), and the last to attain the full count. In the haemulids *Anisotremus virginicus* (Potthoff et al., 1984) and *Haemulon flavolineatum* (Lindeman, 1986) the caudal fin is the first to develop rays but the last to get the full count. In *Microspathodon chrysurus* (Pomacentridae) the caudal fin started to develop rays first together with the pectoral fin, but the caudal fin had adult counts before the pectoral fin (Potthoff et al., 1987). *Archosargus rhomboidalis* (Sparidae) acquired caudal rays long before any other fin differentiated rays, but total counts were closely acquired with all other fins (Houde and Potthoff, 1976). The principal caudal rays in *L. campechanus* articulate with the hypurals, the parhypural, and in half the specimens with the haemal spine of preural centrum 2 (Table 4). Hypural 4 supports the greatest number of principal caudal rays. In the perciforms *Thunnus, Coryphaena,* and *Xiphias,* the haemal spine of preural centrum 2 did not support principal caudal rays (Potthoff, 1975; 1980; Potthoff and Kelley, 1982). The labroid *Microspathodon* also lacked a principal caudal ray on the haemal spine, probably because of the reduced principal caudal ray count (Potthoff et al., 1987). In the perciforms *Archosargus, Scombrolabrax,* and *Anisotremus* the anteriormost ventral principal caudal ray was supported by the haemal spine of the preural centrum 2 (Houde and Potthoff, 1976; Potthoff et al., 1980; 1984). In all the above genera, hypural 4 supported the largest number of principal rays. In *L. campechanus* the caudal complex has the primitive number of percoid parts (Johnson, 1981; 1984) and no fusion exists in adults. Phylogenetic loss and ontogenetic fusion of parts occurred in advanced perciforms, such as in *Elagatis, Thunnus, Coryphaena,* and *Xiphias* (Berry, 1969; Potthoff, 1975; 1980; Potthoff and Kelley, 1982) and is associated with more active swimming (Johnson, 1981). In *L. campechanus,* three centra participate in the support of the caudal rays, which is usual with perciforms. Exceptions to this were found in *Xiphias* where only two centra supported caudal rays (Potthoff and Kelley, 1982) and in a number of scombrid genera where four or five centra participate in the support (Collette and Chao, 1975; Potthoff, 1975; Collette and Russo, 1984; Collette et al., 1984). In *L campechanus,* radial cartilages are absent anterior to the neural and haemal spine of preural centrum 3, as is a procurrent spur in the hypural complex; both indicate a specialization (Johnson, 1975; 1984).

The pectoral fin of *L. campechanus* is the last fin to begin developing rays and the second-to-last to obtain complete counts. In two other lutjanids studied, *Rhomboplites aurorubens* (Laroche, 1977) and *Lutjanus griseus* (Richards and Saksena, 1980), the pectoral fin begins to develop last and is the last completed. This is not the case in other percoids studied so far. Johnson (1984) listed the sequence of completion of fins in percoids but not the sequence of beginning development of fin rays. In *Trachurus* (Carangidae) the pectoral fin was the second fin (caudal was first) to begin ray development, but the last to be completed (Ahlstrom and Ball, 1954). In the haemulids *Haemulon plumieri* and *H. flavolineatum* the pectoral fin started developing next to last (pelvic was last) and was complete next to last (caudal was last) (Saksena and Richards, 1975; Lindeman, 1986). In *Anisotremus* (Haemulidae) the pectoral was the next to last fin (pelvic was last) to acquire rays, but had full counts before the last fin was complete (pelvic was last) (Potthoff et al., 1984). In *Archosargus* (Sparidae) the pectoral fin began development after the caudal simultaneously with the soft dorsal and anal and finished last with the caudal and pelvic fins (Houde and Potthoff, 1976). In *Coryphaena* (Coryphaenidae) the pectoral fin started developing rays second after the caudal fin, but was complete before caudal and dorsal fins (Potthoff, 1980). The development of the pectoral support bones and their anatomy is typically percoid. The development of the pectoral girdle and suspensorium has been recently described for some percoids by Houde and Potthoff (1976), Fritzsche and Johnson (1980), Potthoff (1980), and Potthoff et al. (1984). The adult anatomy of the pectoral girdle of bony fishes, including percoids, has been studied by Starks (1930).

The pelvic fin in *L. campechanus* is second of the fins to develop a spine just after some spines in the spinous dorsal fin appear. It is the first fin to acquire adult counts together with the spinous dorsal and not as Johnson (1984) reported to be the second fin completed. The same sequence of pelvic fin acquisition and completion has been observed in *L. griseus* (Richards and Saksena, 1980). In *Rhomboplites* (Laroche, 1977), acquisition was as in *Lutjanus,* but the pelvic fin was complete first, considerably before all other fins. Leis and Rennis (1983) reported the pelvic fin in the family Lutjanidae to develop and be completed first before all other fins. In other percoid families studied the pelvic fin was always the last to start developing a spine and rays but sequence of completion varied: Carangidae (Ahlstrom and Ball, 1954), Haemulidae (Saksena and Richards, 1975; Potthoff et al., 1984; Lindeman, 1986), Sparidae (Houde and Potthoff, 1976), and Coryphaenidae (Potthoff, 1980). The basipterygium in *L. campechanus* develops only three wings. The fourth ventral wing found in some perciforms studied (*Coryphaena,* Potthoff, 1980; *Scombrolabrax,* Potthoff et al, 1980; *Microspathodon,* Potthoff et al., 1987) is absent in *L. campechanus.* It is not clear if the wing reduction represents the basic state or an advance. We conclude, however, since the basipterygium resembles pterygiophores with four keels, the reduction is an evolutionary advance.

In *L. campechanus* the spinous dorsal, soft dorsal, and anal fins develop from anterior in a posterior direction, except for the anteriormost first dorsal and anal fin spine, which develops later. The development of the soft dorsal and anal fins always follows the completion of the spinous dorsal fin. The spinous dorsal fin is the very first fin to start developing. This kind of fin development sequence is unusual in percoids. Although Johnson (1984) listed only fin completion sequences, these completions can serve as a rough guideline for developmental sequence. Of 73 percoid taxa, only four taxa (inclusive Lutjanidae) completed the spinous dorsal fin before other fins and three more taxa shared spinous dorsal fin completion with soft dorsal fin completion. This uncommon developmental sequence of the spinous dorsal fin in Lutjanidae may be one of many evolutionary responses to early larval predation in the planktonic community. The relatively long and in many species serrated fin spines, when erected, make the larvae appear larger and discourage predators. This speculation is further corroborated by the early development of the pelvic fin, which also has a long, sometimes serrated fin spine. In other percoids the pelvic fin usually develops last. In some scombroids, in which the spinous dorsal fin also developed first, the soft dorsal and anal fins developed differently from the development in *L. campechanus.* In *Scomberomorus, Acanthocybium, Thunnus* and probably in *Sarda,* Potthoff et al. (1986) found that the soft dorsal and anal fins began development at a center and addition was anterior and posterior. In *Istiophorus,* Potthoff et al. (1986) found that the spinous dorsal fin developed first at a center and addition was anterior and posterior for the spinous dorsal and posterior only for the soft dorsal and anal fins.

The predorsal formula of *L. campechanus* is 0/0/0 + 2/1 + 1/, which denotes that there is a predorsal bone in interneural spaces one to three and that interneural space three also has a pterygiophore bearing two supernumerary spines and that interneural space four has two pterygiophores. This formula occurred in 28 percoid taxa (mostly families) out of 96 studied by Johnson (1984). This represents a fairly common occurrence of the formula, when one considers the multitude of other formulae the percoids have. In addition, 66 taxa had three predorsal bones; 64 taxa had one or more members, with the anteriormost pterygiophore having two supernumerary spines; 50 taxa had one predorsal bone in the first, second and third interneural space; in 73 taxa the anteriormost pterygiophore was found in the third interneural space; 49 taxa had two pterygiophores in the fourth interneural space, preceded by one pterygiophore in the first interneural space. Thus *L. campechanus* has the most common arrangement of predorsal bones and pterygiophores in the percoids. Two supernumerary spines and one serially associated spine are present on the first anal pterygiophore in *L. campechanus*. The serially associated spine develops first as a ray and later transforms to a spine. The same development has been observed in the sparid *Archosargus rhomboidalis* (Houde and Potthoff, 1976) and haemulid *Anisotremus virginicus* (Potthoff et al., 1984). In the pomacentrid *Microspathodon chrysurus*, a labroid, the serially associated ray did not transform to a spine (Potthoff et al., 1987), which was considered an advancement (Johnson, 1984). In 96 percoid taxa (mostly families), Johnson (1984) found 79 with two supernumerary spines on the first anal pterygiophore. These two supernumerary spines indicate fusion of two pieces of cartilage to one first anal pterygiophore.

The distal radials of the spinous dorsal fin in *L. campechanus* at first separate from the proximal radial cartilage and then ossify separately. In adults the spinous dorsal fin radials are fused with the proximal radials. It is not known if fusion of spinous dorsal fin distal radials to the proximal radials is common in perciforms. It did not occur in *Thunnus* (Potthoff, 1975), *Scombrolabrax* (Potthoff et al., 1980), *Anisotremus* (Potthoff et al., 1984), or *Microspathodon* (Potthoff et al., 1987). However, in adult *Anisotremus* the distal radials were in an intermediate state of ankylosis.

There are three to five trisegmental pterygiophores in *L. campechanus* in the posterior portion of the soft dorsal and anal fins. We believe that there are more perciform families with trisegmental pterygiophores than without and that bisegmental pterygiophores originate from trisegmental pterygiophores by phylogenetic fusion of the middle radial to the proximal (Eaton, 1945; Lindsey, 1955; Smith and Bailey, 1961). Johnson (1984) showed that in percoids, 54 of 96 taxa (mostly families) had one or more middle radials in the posterior portions of their dorsal and anal fins. *Coryphaena* (Potthoff, 1980), *Xiphias* (Potthoff and Kelley, 1982), *Anisotremus* (Potthoff et al., 1984), and *Haemulon* (Lindeman, 1986) lacked middle radials.

A stay is present in *L. campechanus* behind the posteriormost dorsal and anal pterygiophores. Bridge (1886), Potthoff (1974), and Kohno and Taki (1983) suggested that the stay is a vestigial pterygiophore. Kohno and Taki observed a separate origin of the stay, but the stay originated from the posteriormost pterygiophore cartilage in our study. Most perciforms have stays. Johnson (1984) observed stays in 80 out of 96 percoid groups. Berry (1969) and Potthoff (1980) observed the absence of stays in *Elagatis* and *Coryphaena*.

In *L. campechanus* the hyoid arch develops from three cartilages. From the hypohyal cartilage, two hypohyals ossify; dorsad in the hypohyal cartilage a foramen forms, which is retained in the dorsal hypohyal bone; from the epiceratohyal cartilage the epihyal and ceratohyal bones ossify; only one bone forms from the interhyal cartilage. The same kind of development for the hyoid arch has been observed in the perciforms *Anisotremus* (Potthoff et al., 1984) and *Microspathodon* (Potthoff et al., 1987). *Microspathodon* had the beryciform foramen of McAllister (1968) in the ceratohyal bone, which *Lutjanus* lacked. There were seven branchiostegal rays in *L. campechanus*. This is the most common number of rays in percoids. Johnson (1984) reported seven branchiostegal rays in 54 of 96 percoid taxa.

The adult anatomy of the branchial skeleton of *Lutjanus* has been discussed and compared to other associated groups in detail by Johnson (1981). The development of the branchial skeleton of *Lutjanus* was similar to that of *Anisotremus* (Potthoff et al., 1984).

Development of the upper and lower jaws in perciforms has been little studied. To our knowledge, only Watson (1987) studied jaw development in the blenniid *Enchelyurus brunneolus.*

Acknowledgments

We thank W. D. Anderson, Jr., G. D. Johnson, K. C. Lindeman, and W. J. Richards for reviewing the manuscript. G. L. Morina typed the manuscript and corrected many drafts. The writing of the manuscript and part of the osteological research were done by the first author; the drawings and part of the osteological research were done by the second author; the third author provided and identified the specimens and did some of the osteological research.

Literature Cited

Ahlstrom, E. H. and O. P. Ball. 1954. Description of eggs and larvae of jack mackerel (*Trachurus symmetricus*) and distribution and abundance of larvae in 1950 and 1951. Fish. Bull. Fish. Wildl. Serv. U.S. 56: 209–245.

——— and R. C. Counts. 1955. Eggs and larvae of the Pacific hake *Merluccius productus*. Fish. Bull. Fish. Wildl. Serv. U.S. 56: 295–329.

——— and ———. 1958. Development and distribution of *Vinciguerria lucetia* and related species in the eastern Pacific. Fish. Bull. Fish. Wildl. Serv. U.S. 58: 363–416.

———, J. L. Butler and B. Y. Sumida. 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions, and early life histories and observations on five of these from the northwest Atlantic. Bull. Mar. Sci. 26: 285–402.

Allen, G. R. 1987. Synopsis of the circumtropical fish genus *Lutjanus* (Lutjanidae). Pages 33–87 *in* J. J. Polovina and S. Ralston, eds. Tropical snapper and grouper: biology and fisheries management. Westview Press, Boulder and London.

Arnold, C. R., J. M. Wakeman, T. D. Williams and G. D. Treece. 1978. Spawning of red snapper (*Lutjanus campechanus*) in captivity. Aquaculture 15: 301–302.

Berry, F. H. 1969. *Elagatis bipinnulata* (Pisces, Carangidae): morphology of the fins and other characteristics. Copeia 1969: 454–463.

Bohnsack, J. A. and D. Harper. 1987. Automated Landings Assessment for Responsive Management (ALARM) package for Gulf of Mexico commercial reef fish landings: March 1987 summary. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Coastal Resources Division Contribution No. CRD-86/87-23. 16 pp.

Bradley, E. and C. E. Bryan. 1975. Life history and fishery of the red snapper (*Lutjanus compechanus*) in the northwestern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 27: 77–106.

Bridge, T. W. 1886. The mesial fins of ganoids and teleosts. J. Linn. Soc. London Zool. 25: 530–602.

Collette, B. B. and L. N. Chao. 1975. Systematics and morphology of the bonitos (*Sarda*) and their relatives (Scombridae, Sardini). Fish. Bull. U.S. 73: 516–625.

——— and J. L. Russo. 1984. Morphology, systematics and biology of the Spanish mackerels (*Scomberomorus*, Scombridae). Fish. Bull. U.S. 82: 545–692.

———, T. Potthoff, W. J. Richards, S. Ueyanagi, J. L. Russo and Y. Nishikawa. 1984. Scombroidei: development and relationships. Pages 591–620 *in* H. G. Moser et al., eds. Ontogeny and systematics of fishes. Spec. Publ. 1. Amer. Soc. Ichthyol. Herpetol.

Collins, L. A., J. M. Finucane and L. E. Barger. 1980. Description of larval and juvenile red snapper, *Lutjanus campechanus*. Fish. Bull. U.S. 77: 965–974.

Eaton, T. H., Jr. 1945. Skeletal supports of the median fins of fishes. J. Morph. 76: 193–212.

Emelĭanov, S. W. 1935. Die Morphologie der Fischrippen. Zool. Jahrb., Abt. Anat. Ontog. Tiere 60: 133–262.

Fahay, M. P. 1975. An annotated list of larval and juvenile fishes captured with surface-towed meter net in the South Atlantic Bight during four RV Dolphin cruises between May 1967 and February 1968. NOAA Tech. Rep. NMFS SSRF 685: 1–39.

Fritzsche, R. A. and G. D. Johnson. 1980. Early osteological development of white perch and striped bass with emphasis on identification of their larvae. Trans. Am. Fish. Soc. 109: 387–406.

Gosline, W. A. 1961a. The perciform caudal skeleton. Copeia 1961: 265–270.

———. 1961b. Some osteological features of modern lower teleostean fishes. Smithson. Misc. Collns. 142: 1–42.

Houde, E. D. and T. Potthoff. 1976. Egg and larval development of the sea bream *Archosargus rhomboidalis* (Linnaeus): Pisces, Sparidae. Bull. Mar. Sci. 26: 506–529.

———, W. J. Richards and V. P. Saksena. 1974. Description of eggs and larvae of scaled sardine, *Harengula jaguana*. Fish. Bull. U.S. 72: 1106–1122.

Johnson, G. D. 1975. The procurrent spur: an undescribed perciform caudal character and its phylogenetic implications. Occ. Pap. Calif. Acad. Sci. (121): 1–23.

———. 1981. The limits and relationships of the Lutjanidae and associated families. Bull. Scripps Inst. Oceanogr., Univ. Calif. 24: 1–114.

———. 1984. Percoidei: development and relationships. Pages 464–498 *in* H. G. Moser et al., eds. Ontogeny and systematics of fishes. Spec. Publ. 1. Amer. Soc. Ichthyol. Herpetol.

Kohno, H. and Y. Taki. 1983. Comments on the development of fin supports in fishes. Jap. J. Ichthyol. 30(3): 284–290.

Laroche, W. A. 1977. Description of larval and early juvenile vermillion snapper *Rhomboplites aurorubens*. Fishery Bull. U.S. 75: 547–554.

Leis, J. M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae). Pages 189–237 *in* J. J. Polovina and S. Ralston (eds.). Tropical snapper and grouper: biology and fisheries management. Westview Press, Boulder and London.

——— and D. S. Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. New South Wales University Press, Sidney, Australia and University of Hawaii Press, Honolulu, Hawaii. 269 pp.

Lindeman, K. C. 1986. Development of larvae of the French grunt, *Haemulon flavolineatum*, and comparative development of twelve species of Western Atlantic *Haemulon* (Percoidei, Haemulidae). Bull. Mar. Sci. 39: 673–716.

Lindsey, C. L. 1955. Evolution of meristic relations in the dorsal and anal fins of teleost fishes. Trans. R. Soc. Can. 49 (Ser. 3, Sect. 5): 35–49.

Matsui, T. 1967. Review of the mackerel genera *Scomber* and *Rastrelliger* with description of a new species of *Rastrelliger*. Copeia 1967: 71–83.

McAllister, D. E. 1968. The evolution of branchiostegals and associated opercular, gular, and hyoid bones and the classification of teleostome fishes, living and fossil. Bull. Nat. Mus. Canada 221 (Biol. Ser. No. 77): 1–239.

Monod, T. 1968. Le complexe urophore des poissons téléostéens. Mem. Inst. Fond. Afr. Noire (81): 1–705.

Mori, K. 1984. Early life history of *Lutjanus vitta* (Lutjanidae) in Yuya Bay, the Sea of Japan. Jap. J. Ichthyol. 30: 374–392.

Nagięć, C. 1977. Ossification of the axial skeleton and fins in the whitefish, *Coregonus lavaretus* L. Acta Biologica Cracoviensia, Ser. Zoologia 20(2): 156–180.

Nelson, G. J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. Bull. Am. Mus. Nat. Hist. 141(Art. 4): 475–552.

Nybelin, O. 1963. Zur Morphologie und Terminologie des Schwanzskelettes der Actinopterygier. Ark. Zool. 15: 485–516.

Potthoff, T. 1974. Osteological development and variation in young tunas, genus *Thunnus* (Pisces, Scombridae), from the Atlantic Ocean. Fish. Bull. U.S. 72: 563–588.

———. 1975. Development and structure of the caudal complex, the vertebral column, and the pterygiophores in the black fin tuna (*Thunnus atlanticus*, Pisces, Scombridae). Bull. Mar. Sci. 25: 205–231.

———. 1980. Development and structure of fins and fin supports in dolphin fishes *Coryphaena hippurus* and *Coryphaena equiselis* (Coryphaenidae). Fish. Bull. U.S. 78: 277–312.

———. 1984. Clearing and staining techniques. Pages 35–37 *in* H. G. Moser et al., eds. Ontogeny and systematics of fishes. Spec. Publ. 1. Amer. Soc. Ichthyol. Herpetol.

——— and S. Kelley. 1982. Development of the vertebral column, fins and fin supports, branchiostegal rays and squamation in the swordfish, *Xiphias gladius*. Fish. Bull. U.S. 80: 161–186.

———, ——— and J. Javech. 1986. Cartilage and bone development in scombroid fishes. Fish. Bull. U.S. 84: 647–678.

———, W. J. Richards and S. Ueyanagi. 1980. Development of *Scombrolabrax heterolepis* (Pisces, Scombrolabracidae) and comments on familial relationships. Bull. Mar. Sci. 30: 329–357.

———, S. Kelley, M. Moe and F. Young. 1984. Description of porkfish larvae (*Anisotremus virginicus*, Haemulidae) and their osteological development. Bull. Mar. Sci. 34: 21–59.

———, ———, V. Saksena, M. Moe and F. Young. 1987. Description of larval and juvenile yellowtail damselfish *Microspathodon chrysurus*, Pomacentridae, and their osteological development. Bull. Mar. Sci. 40: 330–375.

Rabalais, N. N., S. C. Rabalais and C. R. Arnold. 1980. Description of eggs and larvae of laboratory-reared red snapper (*Lutjanus campechanus*). Copeia 1980: 704–708.

Richards, W. J. R. and V. P. Saksena. 1980. Description of larvae and early juveniles of laboratory-reared gray snapper, *Lutjanus griseus* (Linnaeus) (Pisces, Lutjanidae). Bull. Mar. Sci. 30: 516–521.

———, R. V. Miller and E. Houde. 1974. Egg and larval development of the Atlantic thread hearing, *Opisthonema oglinum*. Fish. Bull. U.S. 72: 1123–1136.

Rivas, L. R. 1966. Review of the *Lutjanus campechanus* complex of red snappers. Q. J. Fl. Acad. Sci. 29(2): 117–136.

Rosen, D. E. 1973. Interrelationships of higher euteleostean fishes. Pages 397–513 *in* P. H. Greenwood, R. S. Miles, and C. Patterson, eds. Interrelationships of fishes. Supplement No. 1 to the Zoological Journal of the Linnean Society Vol. 53. Academic Press, London, New York.

Saksena, V. and W. J. Richards. 1975. Description of eggs and larvae of laboratory-reared white grunt, *Haemulon plumieri* (Lacépède) (Pisces, Pomadasyidae). Bull. Mar. Sci. 25: 523–536.

Smith, C. L. and R. M. Bailey. 1961. Evolution of the dorsal fin supports of percoid fishes. Pap. Mich. Acad. Sci. Arts Lett. 46: 345–363.

Starks, E. C. 1930. The primary shoulder girdle of the bony fishes. Stanford Univ. Publ. Biol. Sci. 6: 147–240.

Suzuki, K. and S. Hioki. 1979. Spawning behavior, eggs, and larvae of the lutjanid fish, *Lutjanus kasmira*, in an aquarium. Jap. J. Ichthyol. 26: 161–166.

Watson, W. 1987. Larval development of the endemic Hawaiian blenniid, *Enchelyurus brunneolus* (Pisces: Blenniidae: Omobranchini). Bull. Mar. Sci. 41.

DATE ACCEPTED: October 5, 1987.

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